Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia) 4. *Palaemon (Palaemon) serratus* (Pennant, 1777) and functional morphology of swimming

A. A. Fincham

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

Palaemonid shrimps are widely distributed in the N.E. Atlantic being found in fresh water, in estuaries, intertidally and down to 40 m offshore, but their larvae are rare in the plankton. All decapod larvae have a natural tendency to sink (Foxon, 1934) and in order to maintain position at a particular depth (Savage, 1926) and perform daily vertical migrations (Russell, 1925, 1927; Hardy & Bainbridge, 1954), active upward swimming is necessary also. Foxon measured rates of movement in various decapods including pandalid carideans and several authors have noted the effect of light and gravity on the orientation and movement of decapod larvae (Sollaud, 1921; Gurney, 1942; Forward & Cronin, 1978).

The aim of this paper is to review the larval development of *Palaemon (Palaemon) serratus* (Pennant, 1777) and report on morphological adaptations, and a mechanism using many-jointed plumose setae fringing the thoracic exopods, for larval swimming.

Materials and Methods

Rearing

Ovigerous *Palaemon (Palaemon) serratus* were trawled from 12 m in April 1979 from Plymouth Sound, Devon (Grid reference: SX 475512). Similar rearing techniques to those reported previously (Fincham 1977, 1978, 1979) were used with the following modifications:
1. The controlled temperature room was at 14 °C.
2. Antibiotics were used for the first three stages only (Fincham, 1979).
Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1982 : 186.

Telson morphology

The telson was removed from larvae by a cut at the narrow junction with the abdomen, rinsed in distilled water, freeze dried, mounted end-on with Araldite on stubs, coated with gold and examined with a scanning electron microscope.

Palaemon (Palaemon) serratus (Pennant, 1777)

Astacus serratus Pennant, 1777
Melicerta triliana Risso, 1816
Palaemon trilianus Risso, 1826
Palaemon treillianus H. Milne Edwards, 1837
Leander latreillianus Czerniavsky, 1884

Bull. Br. Mus. nat. Hist. (Zool.) **44**(2): 125–161 Issued 24 February 1983

Table 1 Larval development and range of morphological and meristic variation in *Palaemon (Palaemon) serratus*
R = rudimentary; + = present/yes; − = absent/no; W = wide; N = narrow

	Zoea/Moult									
	1	2	3	4	5	6	7	8	9	PL1
Carapace										
No. of dorsal spines	0	1	2	3	3	3	3	3	3	7(3)[1]
No. of ventral rostral spines	0	0	0	0	0	0	0	0	0	2(0)[1]
Supraorbital spines +/−	−	+	+	+	+	+	+	+	+	−(+)[1]
No. of antero-lateral spines	0	1	1	2	2	2	2	2	2	2
Rostrum tip – downturned +/−	−	+	+	+	+	+/−	+/−	+/−	−	−
Ventral retrorse hooks +/−	+	−	−	−	−	−	−	−	−	−
	One group					two or more groups				
Antenna 1	1W,2N	2W,2N	3W	3W,1N	3W,1N	3W,1N 2 or 3N	4W 3N (1N)	2–3 groups	3–4 groups	4 or more
Stylocerite +/−	−	R	+	+	+	+	+	+	+	+
Statocyst +/−	−	−	−	−	R	R	R	R	+	+
No. of segments flagellum internal	0	0	1	1	1	1	1	1	1–2	5
external	1	1	1	1	1	1	1	1	2	7
Accessory flagellum +/−	−	−	−	−	−	−	−	−	−	R
Antenna 2										
Endopodite – No. of segments	1	1	3	3	3–4	4–5	5–7	6–7	9–12	many
Length of scapthocerite	0·64:1 to 0·71:1	0·65:1 to 0·74:1	0·69:1 to 0·75:1	0·75:1 to 0·81:1	0·80:1 to 0·88:1	<	=	=	>	>
Exopodite – No. of distal segments	5	4–5	3	0	0	0	0	0	0	0
No. of plumose setae	9+2	15+2 to 17+2	19+2 to 21+2	22+2 to 24+2	24–26	28–31	29–32	31–34	35–39	⩾40
External spine +/−	−	−	−	−	−	−	−	−	−	+
Mandible – Lacinia mobilis +/−	+	+	+	+	+	+	+	+	+	−
Palp	−	−	−	−	−	−	−	−	−	−
Maxilla 1										
No. of endite setae – Coxa	6	6	6	7	7	7–8	7–8	7–8	8–9	>9
Basis	5	7	7	8	8	8–9	8–9	8–9	9–13	⩾13

Maxilla 2										
No. of endite setae – Coxa	4	4	4	4	4	4	4	4	4	0
Basis 1	3	3	3	3	3	3–4	4	4	4–5	10
Basis 2	4	4	4	4	4	4	4–6	4–6	6	>12
Endopodite	3	3	3	3	3	3	3	3	3	2
No. of plumose setae exopodite	5	7–8	10–12	12–14	16–18	19–22	21–25	23–31	26–35	>40
Maxilliped 1										
No. of setae on internal margin – Coxa	1	1	1	1	1	1	1	1	1	8
Basis	6	6	6	7	7	9	9–10	11–13	14–20	>30
Exopodite – No. of setae – Lateral	0	0	0	0	0	1	2–5	5–6	5–9	⩾9
Maxilliped 2										
Endopodite – No. of segments	4	4	4	4	4	4	4	4	4	5
Exopodite +/–	+	+	+	+	+	+	+	+	+	+
Setae +/–	+	+	+	+	+	+	+	+	+	+
Maxilliped 3										
Endopodite – No. of segments	4	5	5	5	5	5	5	5	5	5
Exopodite +/–	+	+	+	+	+	+	+	+	+	+
Setae +/–	+	+	+	+	+	+	+	+	+	+
Pereiopods 1 & 2 +/–	R	+	+	+	+	+	+	+	+	+
Biramous +/–	+	+	+	+	+	+	+	+	+	R
Endopodite – Propodus fixed finger +/–	–	–	–	–	+	+	+	+	+	+
Pereiopod 3 +/–	–	R	R	+	+	+	+	+	+	+
Biramous +/–		+	+	+	+	+	+	+	+	+
Pereiopod 4 +/–	–	R	R	R	+	+	+	+	+	+
Biramous +/–		+	+	+	+[2]	+[3]	+[3]	+	+	+
Pereiopod 5 +/–	–	R	R	+	+	+	+	+	+	+
Biramous +/–		–	–	–	–	–	–	–	–	–
Abdomen										
Somite 5 – lateral spines +/–	–	+	+	+	+	+	+	+	+	+
Somite 6 – 'Continuous' with telson +/–	+	+	–	–	–	–	–	–	–	–
Pleopods +/–	–	–	–	–	R	R	R	R	+	+
Fringing setae					–	–	–	+/–	+/–	+
Appendix interna 2–5 +/–					–	–	–	–	+	+
Telson										
Posterior margin concave (–) or convex (+)	+/–	+/–	–	–	–	–	+/–	+	+	+
Spine formula	7+7	7+7	[1]6+6[1]	[3]4+4[3]	[3]4+4[3]	[3]4+4[3]	[3]4+4[3]	4+4	4+4	4+4
Small spines +/–	+	+	+	+	+	+	+	+	–	–
No. prs. of lateral spines	0	0	0	0	0	0	0	3	3	3
Uropods +/–	–	–	+	+	+	+	+	+	+	+
Long plumose setae – Endopodite			0	9–12	13–16	18–21	18–23	19–27	24–33	>36
Expodite			11–12	18–19	21–24	26–29	27–31	28–32	31–36	>39

[1]intermediate form; [2]rudimentary fringing setae; [3]reduced fringing setae or of normal length.

Leander serratus Sharp, 1893
Leander treillianus Adensamer, 1898
Leander serratus var. *treillianus* De Man, 1915
Palaemon (Palaemon) serratus Holthuis, 1950

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. Thompson, 1836 zoeae I, III & V, p. 221, Figs 1–5, laboratory reared and plankton. Couch, 1845 zoea I, p. 20, no Figs, laboratory reared. Mayer, 1877 zoea I, telson, p. 250, Fig. 49. Keeble and Gamble, 1904 zoea I, chromatophores, p. 316. Sollaud, 1912 zoeae I–IX, p. 664, no Figs, laboratory reared. Williamson, 1915 zoea II (not I), Figs 120–125, zoea I Figs 126–128, last zoea Figs 129–132, p. 396, plankton. Sollaud, 1923 zoeae I–IX & post larva I, p. 530, plates 16–18 (Figs 1–4 only), laboratory reared and plankton. Reeve, 1969 zoeae I–V (XI), p. 77, no Figs, laboratory reared. Sutton *et al.*, 1969 zoea I, counting larvae, p. 433, Fig. 1, laboratory reared. Fincham & Williamson, 1978 key to larval stages.

In the following short descriptions of the key characters of the larval stages, setal counts have been omitted usually, but they are recorded in Table 1.

Description of larval stages

Key characters are printed in *italic type* and are useful for separating stages in British species.

ZOEA 1 (Fig. 1) 3·3 mm (3·2–3·5 mm)

Head (Figs 1a, b): *eyes sessile.*
Carapace (Figs 1a, b): *without spines,* rostrum straight or downcurved at tip, tapering distally, ventral margin with minute retrorse teeth distally, *equal to, or greater than, length of peduncle of antenna 1 but not reaching to end of antenna 1* (excluding terminal aesthetascs and setae).
Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, usually two narrow and one wide, occasionally 1 narrow and 2 wide.
Antenna 2 (Fig. 1d): exopodite as a broad lamina divided into 5 short segments distally, with 9+2 plumose setae on inner and distal margins. Endopodite of one segment (0·67 length of exopodite), with terminal plumose seta and short spine.
Mandibles (Fig. 1e): asymmetrical.
Maxillipeds 1–3 (Figs 1h–j): with natatory exopodites.
Pereiopods 1, 2 (Figs 1k, l): *rudimentary, biramous.*
Pereiopods 3–5: absent.
Abdomen (Figs 1a, b): *somite 5 with posterior margin rounded,* not produced into spines, somite six continuous with telson. No trace of pleopods.
Telson (Fig. 1p): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost spines.

ZOEA 2 (Fig. 2) 3·7 mm (3·5–3·9 mm)
Head (Figs 2a, b): *eyes stalked.*
Carapace (Figs 2a, b): *one dorso-medial and a pair of supra-orbital spines* all bent forward with small retrorse teeth, *rostrum without teeth, downturned at end to form small hook.*
Antenna 1 (Fig. 2c): *two peduncle segments, stylocerite forming on proximal external margin of first segment; single flagellar segment with four terminal aesthetascs, two wide and two narrow.*
Antenna 2 (Fig. 2d): exopodite with 4 or 5 short segments distally.
Pereiopods 1, 2 (Figs 2k, l): *developed with natatory exopodite.*
Pereiopods 3, 4 (Figs 2m, n): *rudimentary, biramous.*
Pereiopod 5 (Fig. 2o): *rudimentary, uniramous.*
Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of conspicuous spines, somite 6 continuous with telson.*
Telson (Fig. 2p): *developing uropods visible beneath exoskeleton* alongside telson proper; *in central group of small spines, one pair longer than others.*

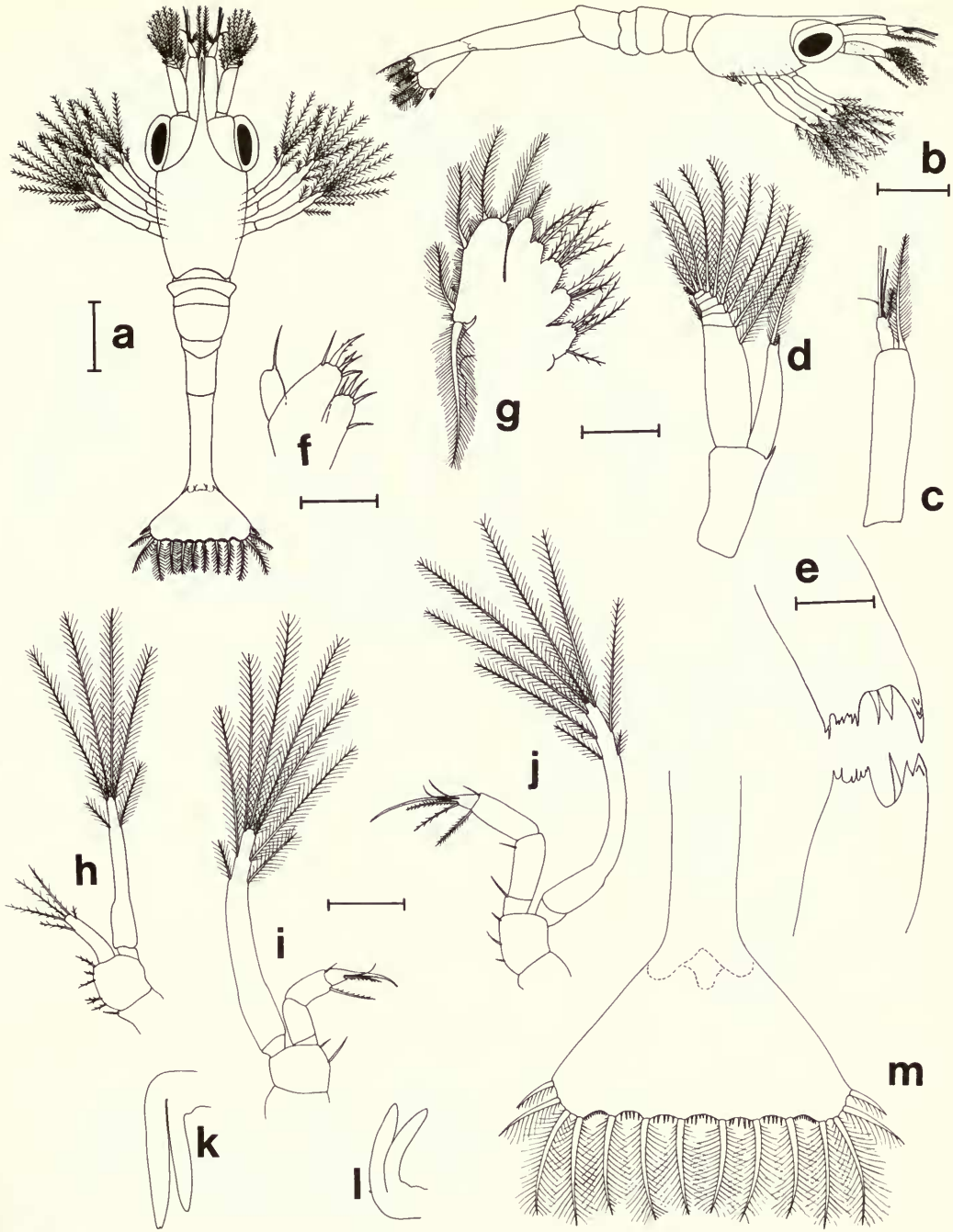

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) telson. Bar scales: a, b=0·5 mm; c, d, h–m=0·2 mm; g, f= 0·1 mm; e=0·05 mm.

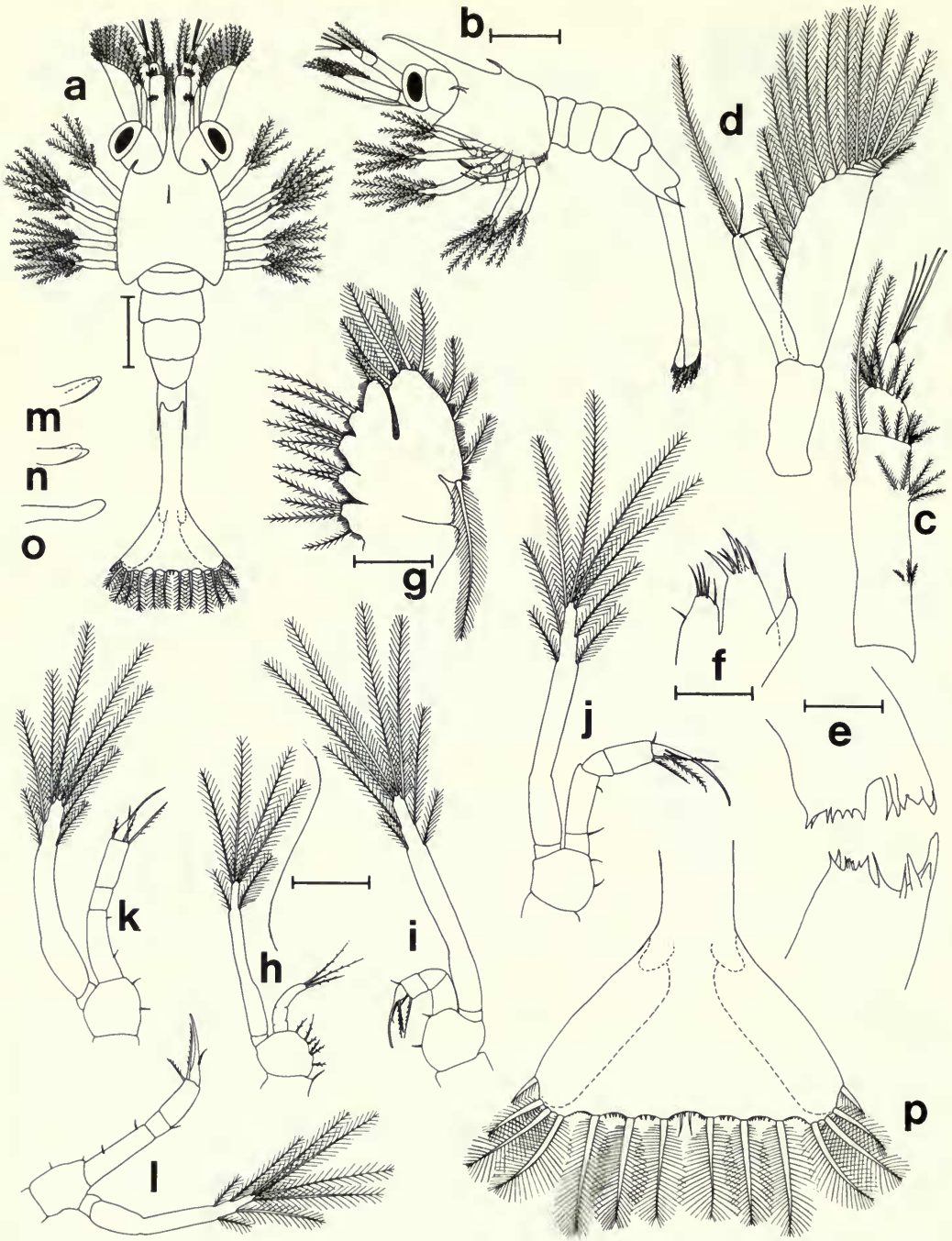

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h–p = 0·2 mm; g, f = 0·1 mm; e = 0·05 mm.

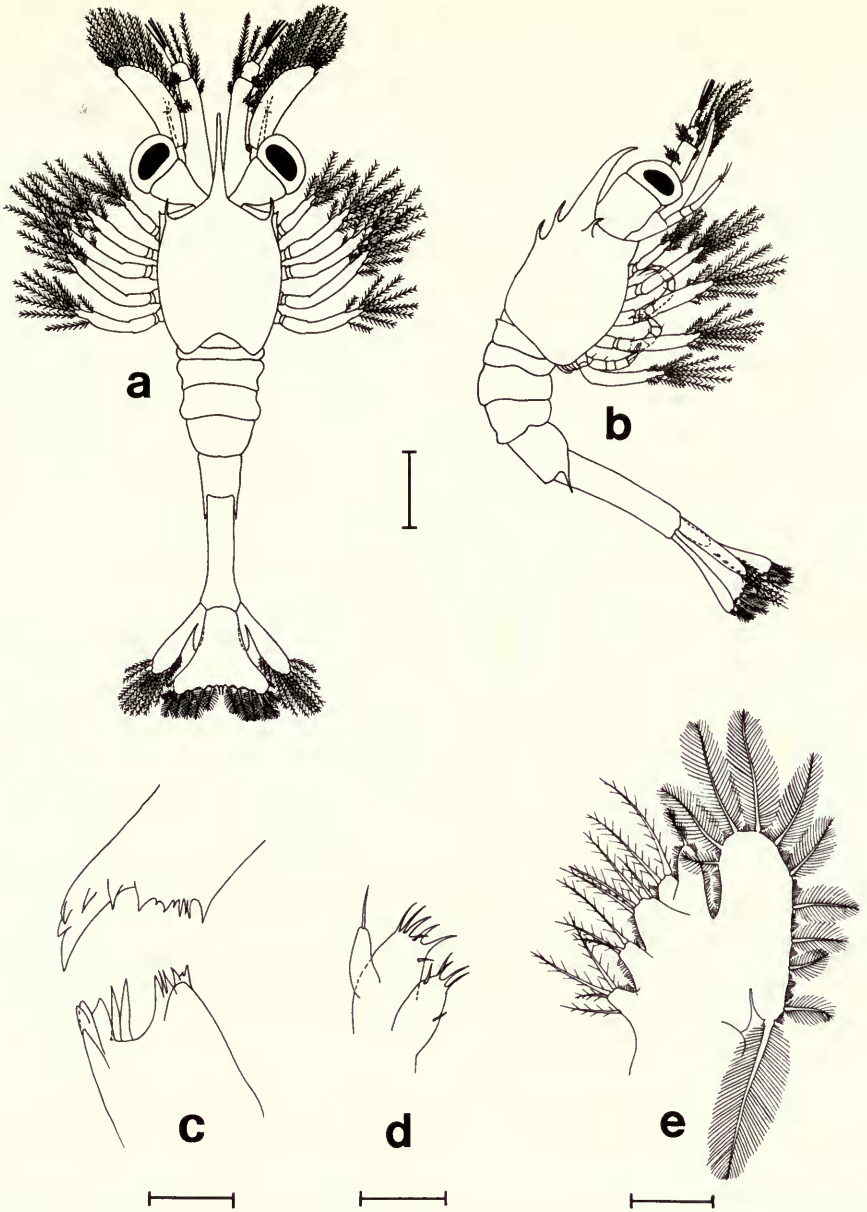

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

ZOEA 3 (Figs 3, 4) 4·0 mm (3·7–4·3 mm)
Carapace (Fig. 3a, b): *two dorso-medial spines* and a small fronto-lateral spine at edge of carapace beneath the eyes, former with retrorse teeth ventrally.
Antenna 1 (Fig. 4a): *conspicuous spine medially,* stylocerite more pronounced; distal segment of peduncle bearing *first segment of internal flagellum,* single segment of *external flagellum bearing 3 wide aesthetascs distally.*
Antenna 2 (Fig. 4b, c): exopodite with distal part divided into 3 short segments; *endopodite of 3 segments.*

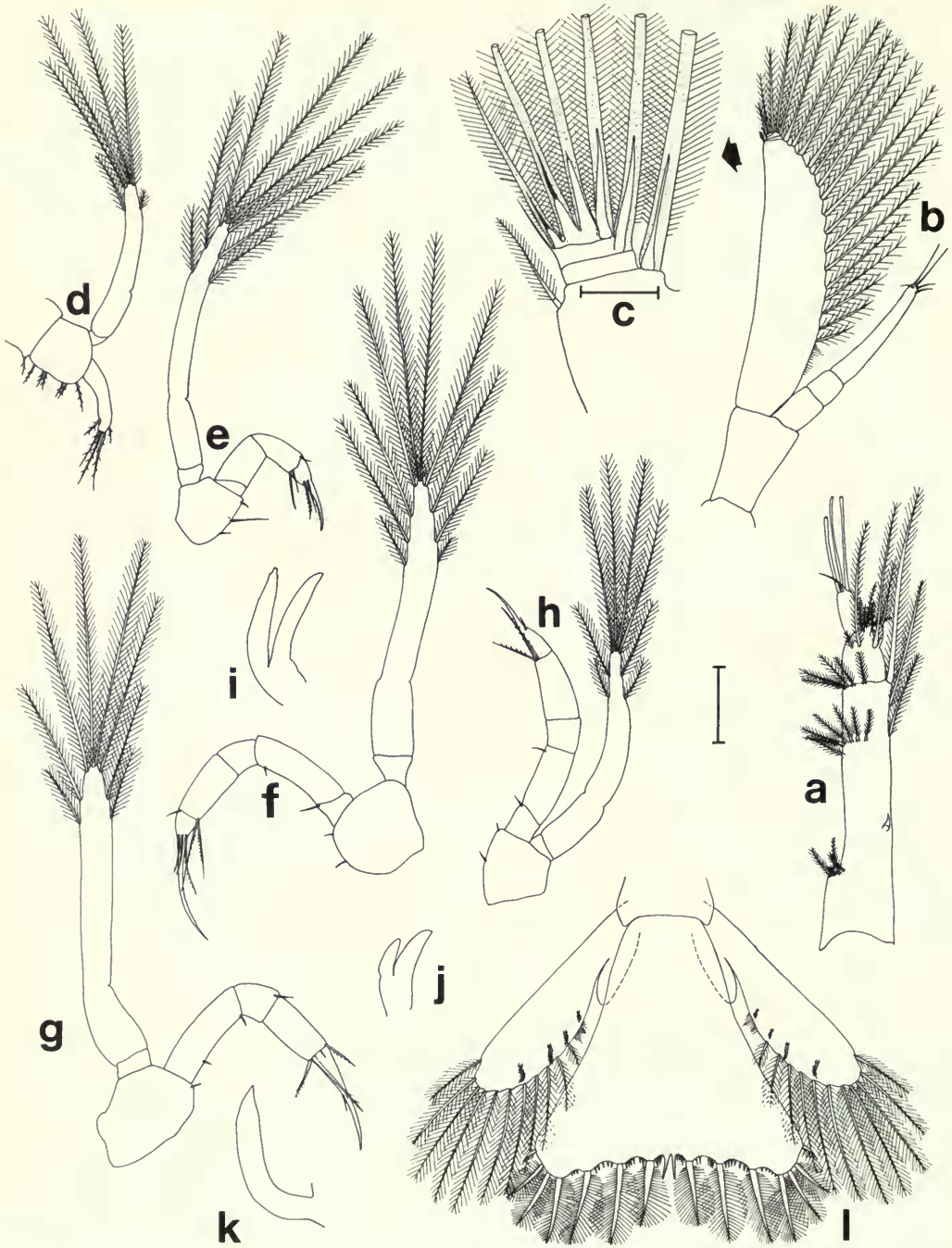

Fig. 4 Zoea 3: (a) antenna 1; (b) antenna 2; (c) distal part of exopodite of antenna 2; (d) maxilliped 1; (e) maxilliped 2; (f) maxilliped 3; (g) pereiopod 1; (h) pereiopod 2; (i) pereiopod 3; (j) pereiopod 4; (k) pereiopod 5; (l) telson. Bar scales: a, b, d–l = 0·2 mm; c = 0·05 mm.

Abdomen (Figs 3a, b, 4l): *somite 6 divided from telson by suture. Uropod endopodite rudimentary with no marginal setae, exopodite with marginal setae.*
Telson (Fig. 4l): narrower but still broader distally, outer pair of spines on posterior margin reduced.

Zoea 4 (Figs 5, 6) 4·5 mm (4·1–5·0 mm)
Carapace (Fig. 5a, b; Fig. 6a, b): *three dorso-medial spines* with retrorse teeth ventrally; pair of small fronto-lateral spines at edge of carapace beneath the eyes; *rostrum still downturned at end to form a small hook.*
Antenna 1 (Fig. 5c): *single segment of external flagellum bearing 3 wide and 1 narrow aesthetascs distally.*
Antenna 2 (Fig. 5d): distal part of exopodite no longer divided into segments.
Pereiopod 3 (Fig. 6h): *developed with natatory exopodite.*
Pereiopod 4 (Fig. 6i): *rudimentary, biramous.*
Pereiopod 5 (Fig. 6j): *developed, uniramous.*
Abdomen (Figs 5a, b): *endopodite and exopodite of uropod both with marginal plumose setae.*
Telson (Fig 6k): narrower but still broader distally; posterior margin weakly concave with *4+4 large spines,* the 3 outer spines on the latero-distal margin reduced (outer pair sometimes absent).

Zoea 5 (Figs 7–9) 5·5 mm (5·2–5·8 mm)
Carapace (Figs 7a, b): *rostrum still downturned to form a small hook.*
Antenna 1 (Fig. 8a): *rudiment of circular statocyst visible on first segment of peduncle.*
Antenna 2 (Fig. 8b): *endopodite of 3 or 4 segments.*
Pereiopods 1, 2 (Figs 9a, b): *endopodite with internal distal margin of propodus produced slightly forward* (will become fixed finger of chela).
Pereiopod 4 (Fig. 9d): *developed, exopod with rudimentary fringing setae.*
Telson (Fig. 9f): a little broader distally than proximally; spine formula as in Zoea 4 but with further reduction or even loss of small outer spines.
Abdomen (Fig. 7b): *somites 1–5 with rudimentary pleopods.*

Zoea 6 (Figs 10–12) 5·7 mm (5·2–7·4 mm)
Carapace (Figs 10a, b): rostrum weakly hooked at tip; *short plumose seta in angle of anterior dorso-medial spine.*
Antenna 1 (Fig. 11a): single external flagellum with four aesthetascs distally, *additional group of 2 or 3 narrow aesthetascs on internal margin.*
Antenna 2 (Fig. 11b): increase in number of segments of endopodite flagellum, *approximately equal to scaphocerite in length,* small spine on distal margin of peduncle segment.
Maxilla 2 (Fig. 11e): occasional increase in number of setae on basis 1.
Maxilliped 1 (Fig. 11f): *one plumose seta on proximo-lateral margin of exopod.*
Pereiopods 1, 2 (Figs 12a, b): *endopodite with internal distal margin of propodus produced foreward to almost half length of dactylus* (excluding terminal setae).
Pereiopod 4 (Fig 12d): exopodite occasionally with fringing plumose setae reduced.
Abdomen (Fig. 10b): pleopods on somites 1–5 rudimentary, biramous.

Zoea 7 (Figs 13–15) 6·1 mm (5·5–6·7 mm)
Carapace (Figs 13a, b): rostrum straight or weakly hooked at tip; *2 or 3 short plumose setae in angle of anterior dorso-medial spine.*
Antenna 1 (Fig. 14a): two or occasionally three groups of aesthetascs on internal margin of external flagellum.
Maxilla 2 (Fig. 14e): up to 6 setae on basis 2.
Maxilliped 1 (Fig. 14f): *2–5 plumose setae on proximo-lateral margin of exopodite.*
Pereiopods 1, 2 (Figs 15a, b): endopodite with internal distal margin produced forward to half length of dactylus (excluding terminal setae).

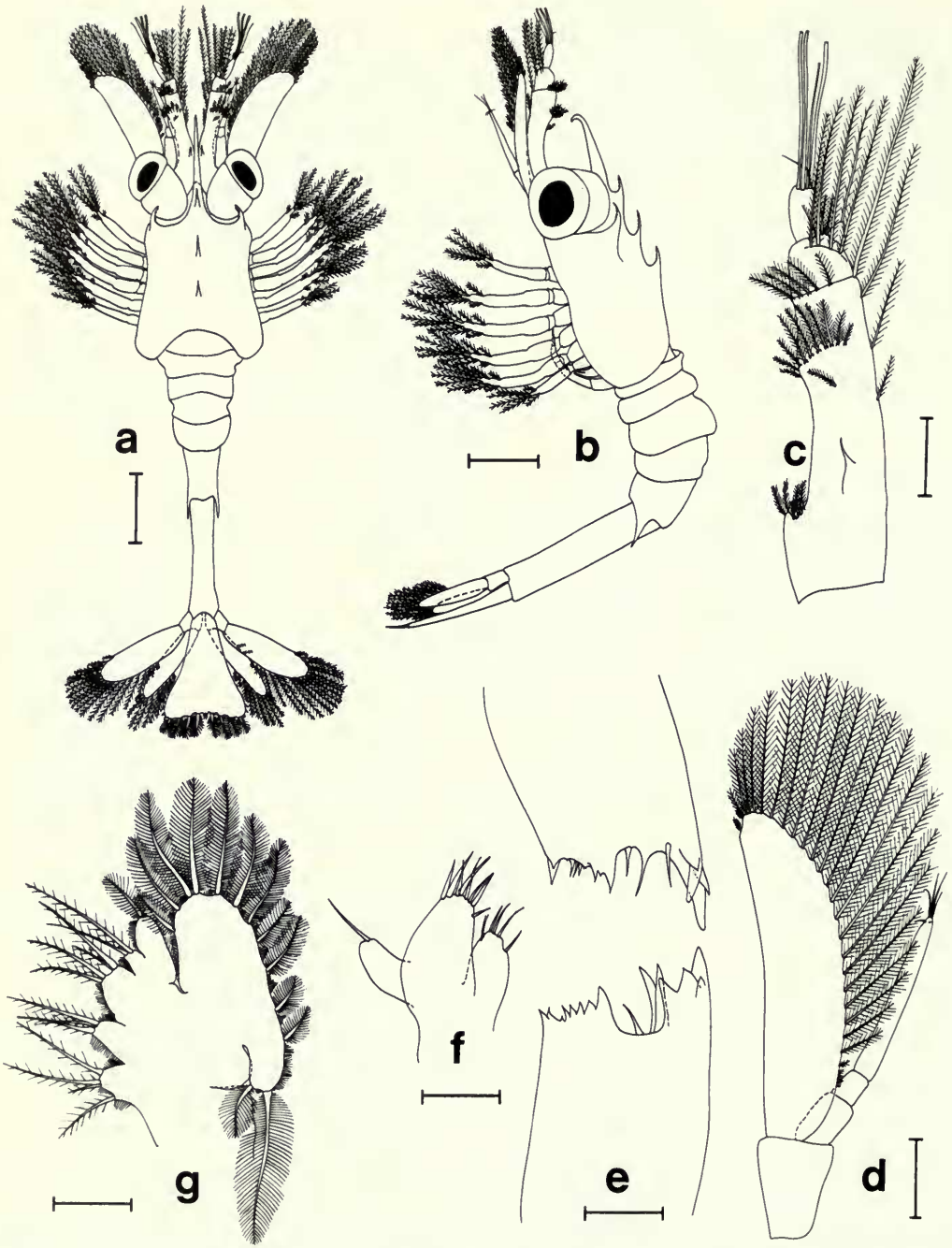

Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

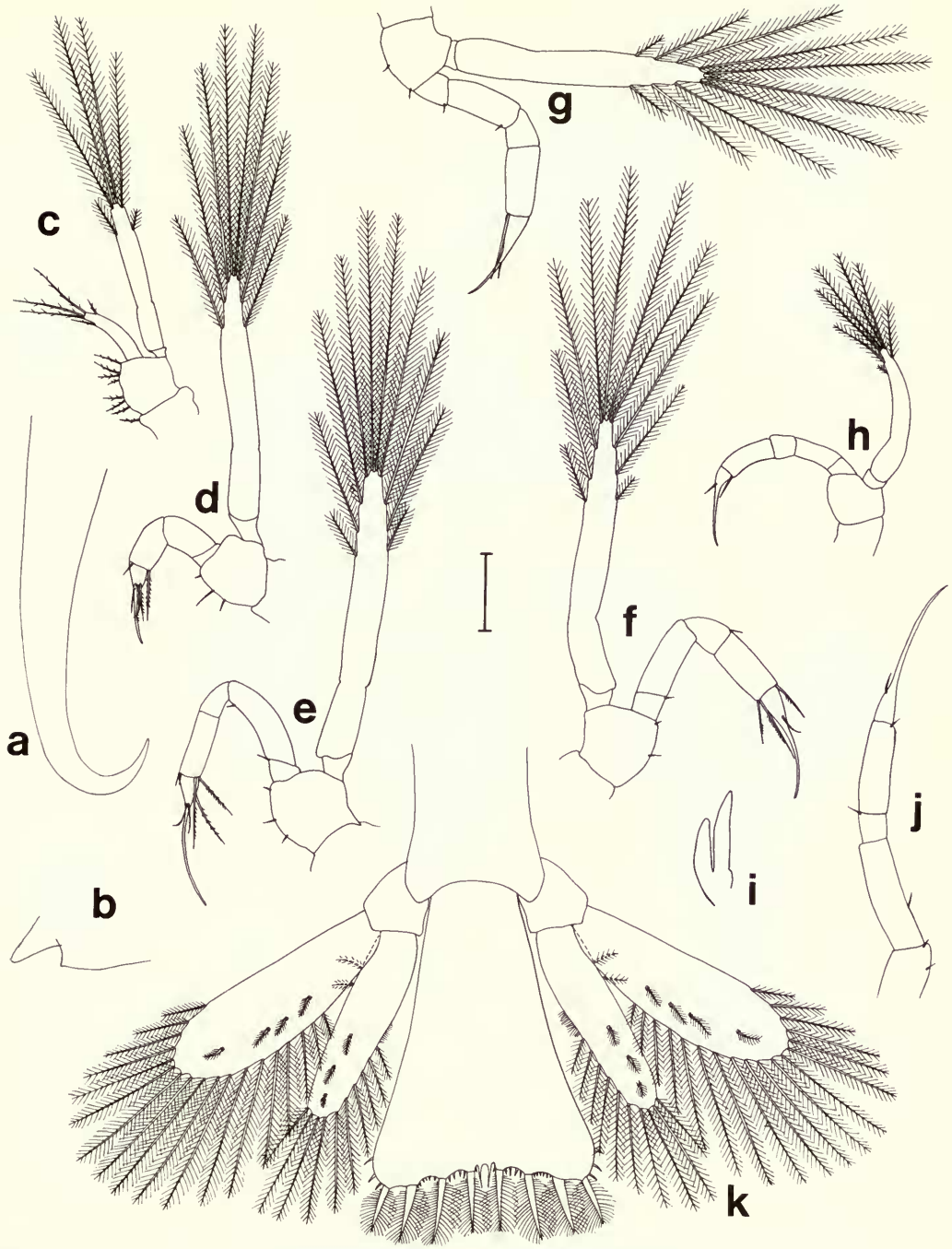

Fig. 6 Zoea 4: (a) tip of rostrum; (b) fronto-lateral corner of carapace; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scales: a, b = 0·05 mm; c–k = 0·2 mm.

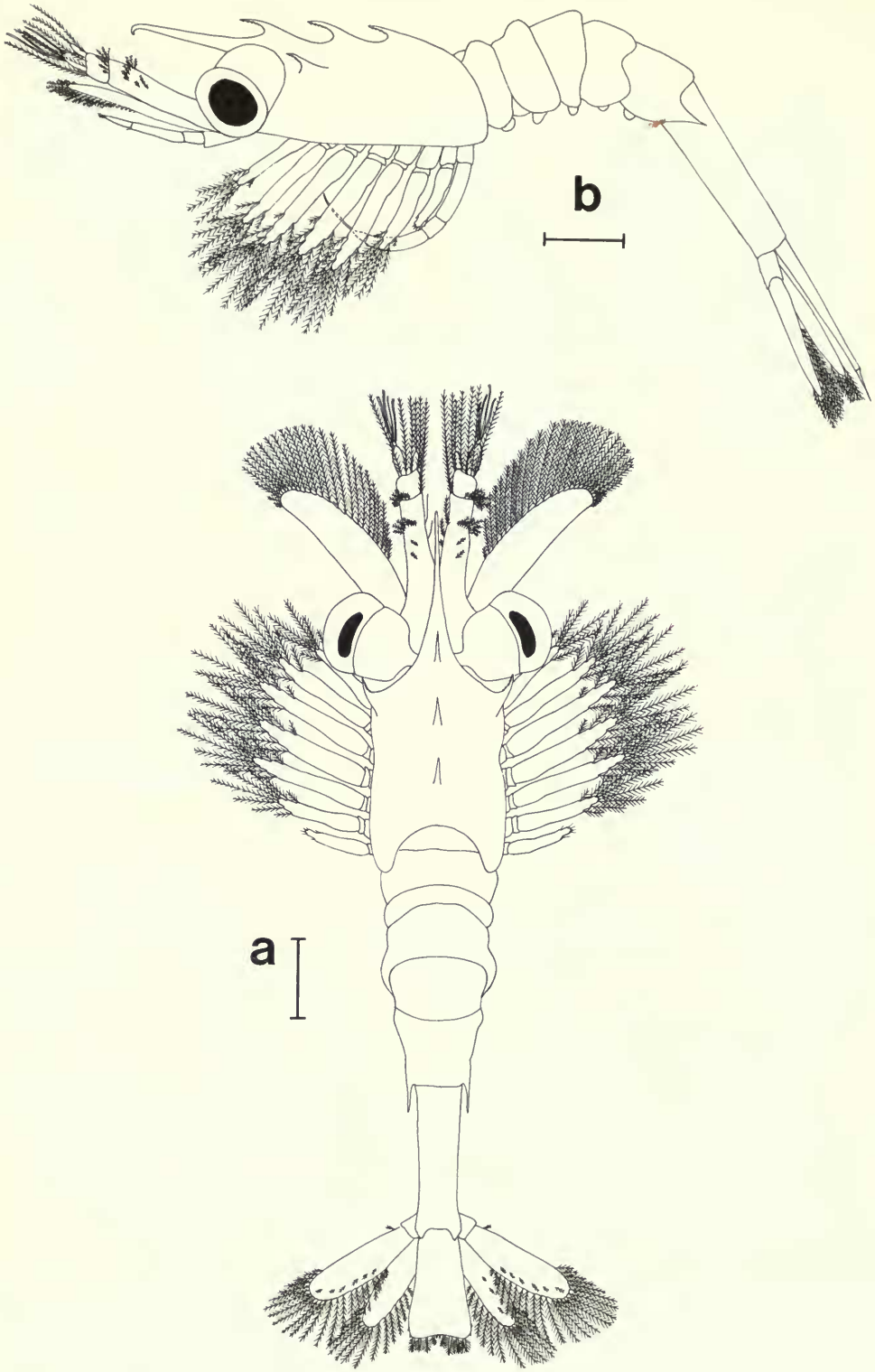

Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

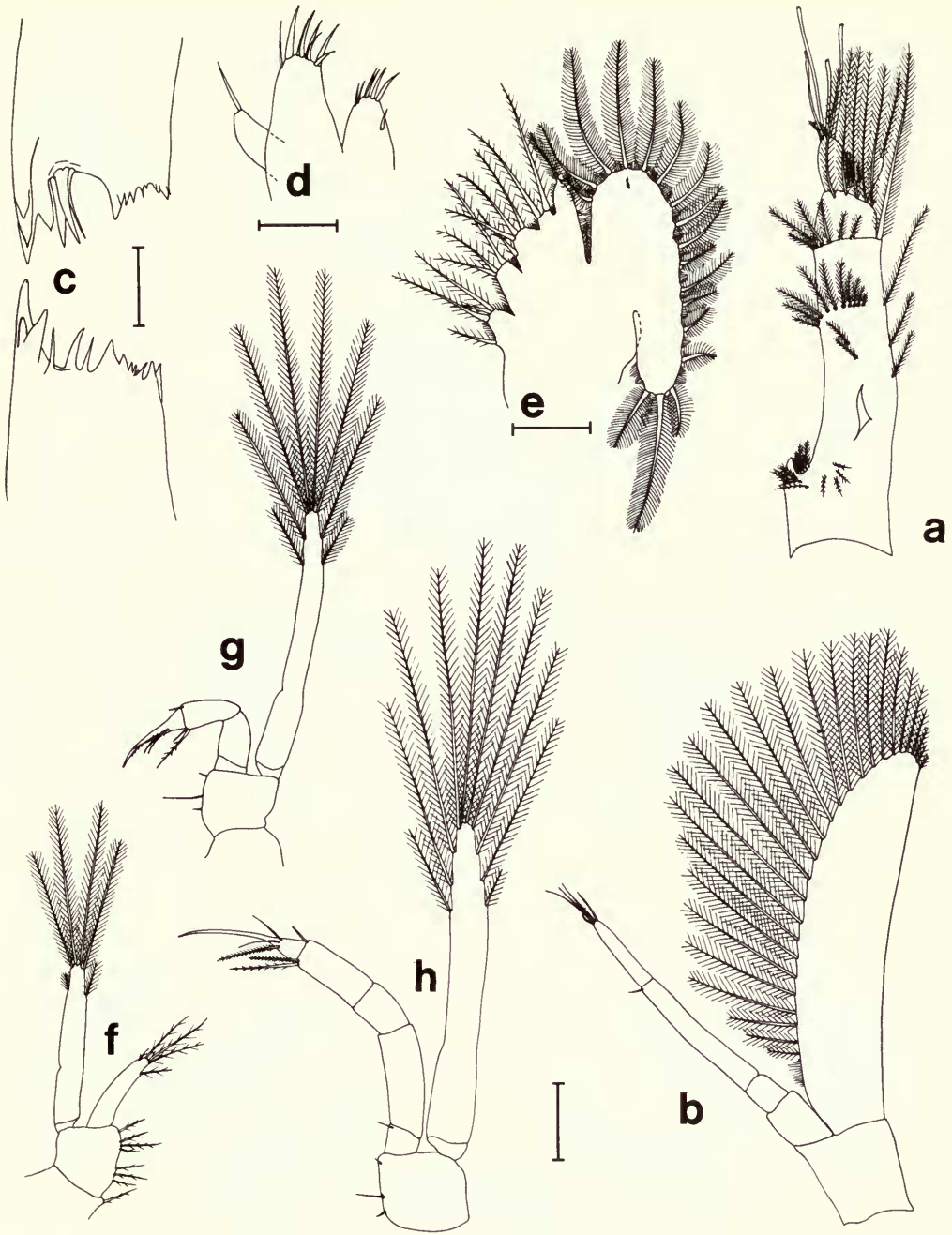

Fig. 8 Zoea 5: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

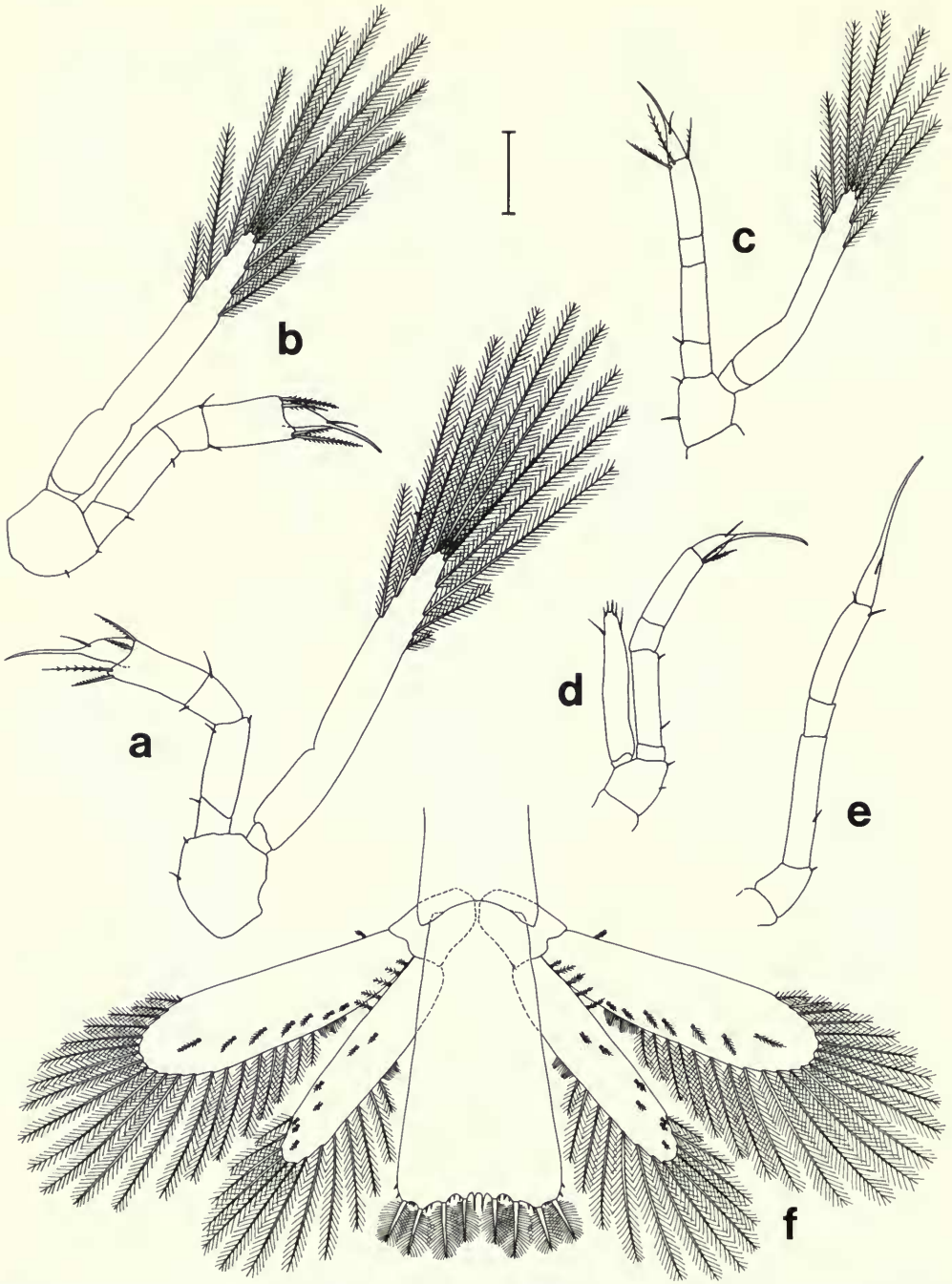

Fig. 9 Zoea 5: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) telson. Bar scale: 0·2 mm.

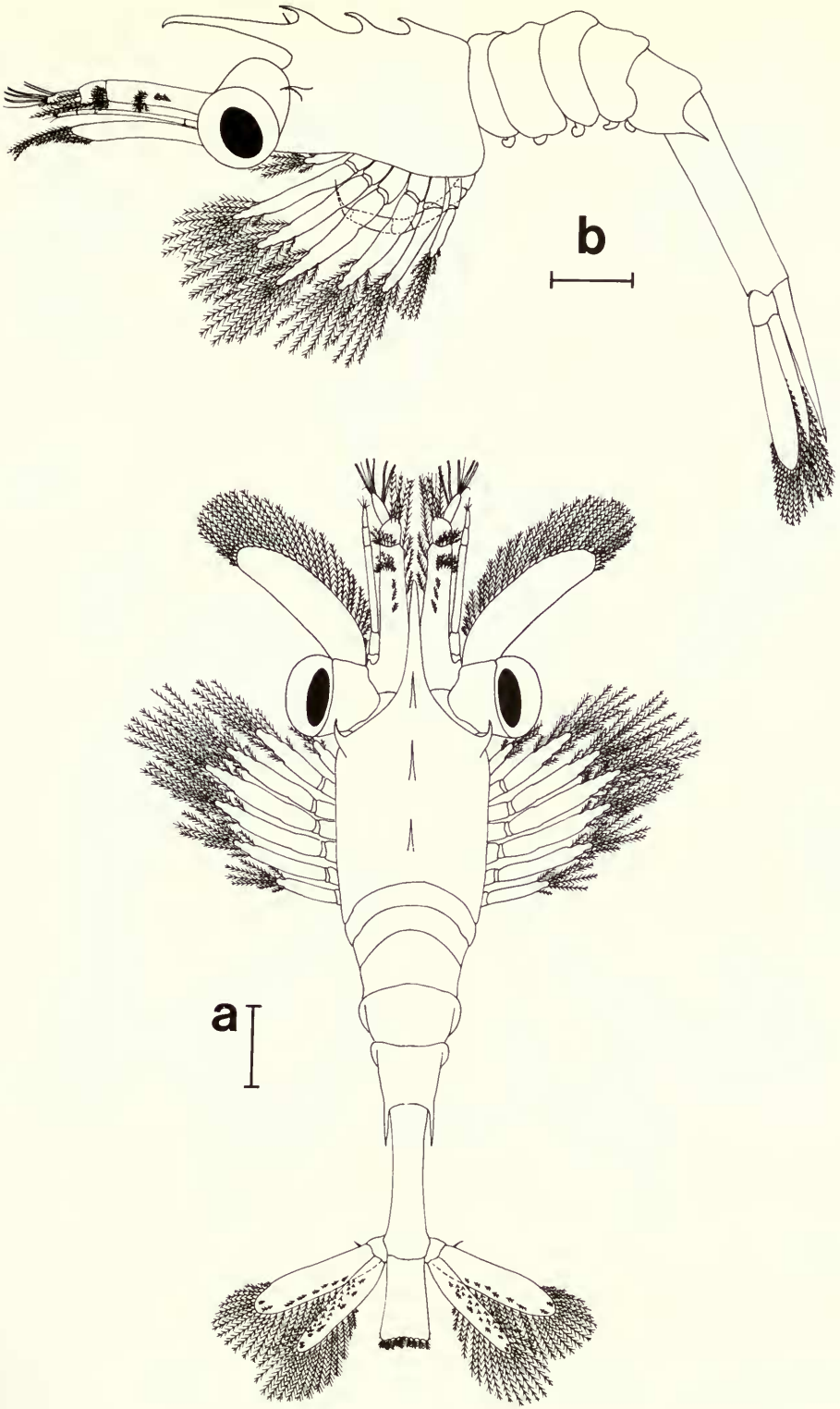

Fig. 10 Zoea 6: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

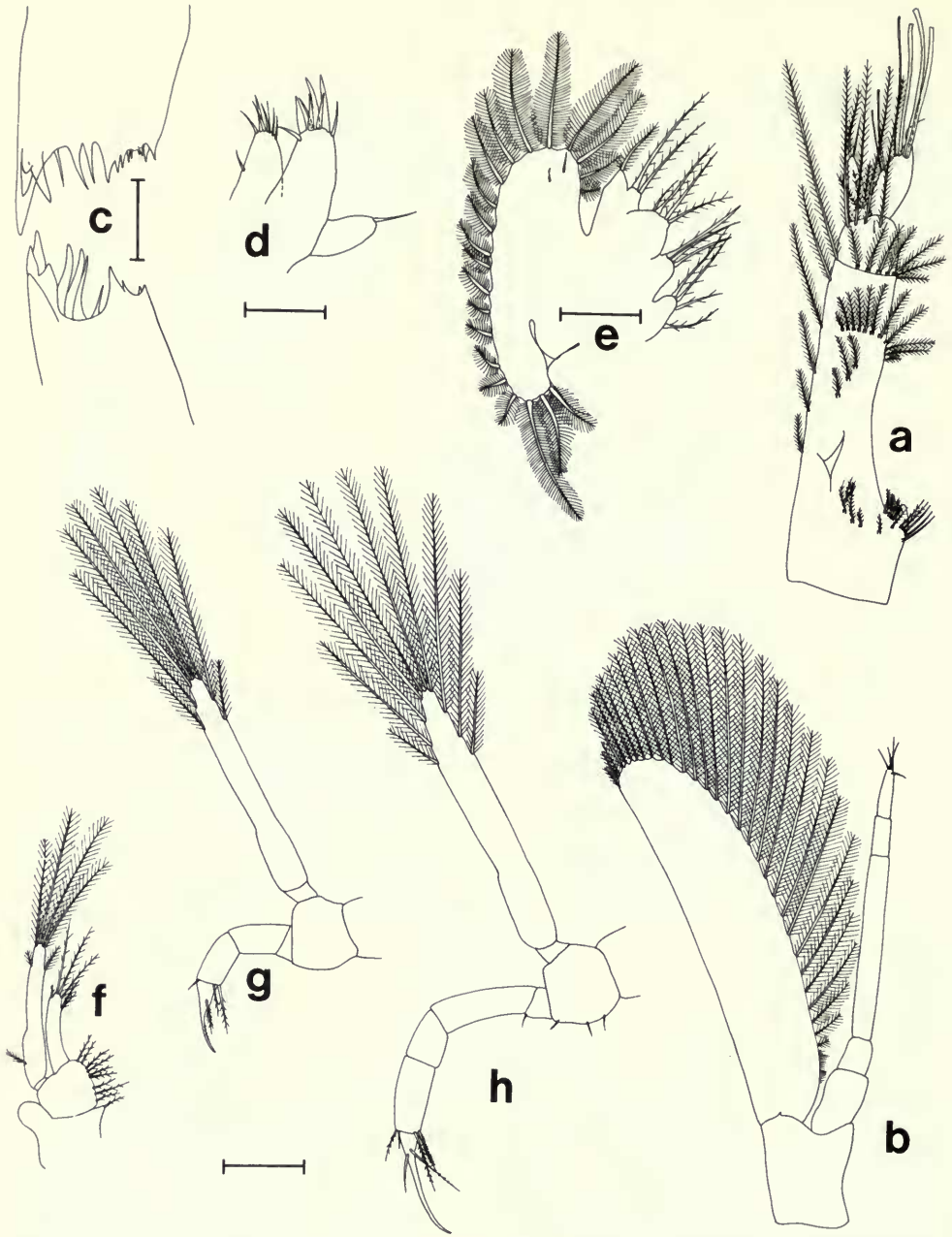

Fig. 11 Zoea 6: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

Pereiopod 4 (Figs 15d, e): exopodite occasionally with fringing plumose setae much reduced.
Abdomen (Figs 13b, 15g–k): pleopods 1–5 still rudimentary, biramous with traces of terminal setae on exopodites.
Telson (Figs 13a, 15l): *posterior margin straight or slightly convex.*

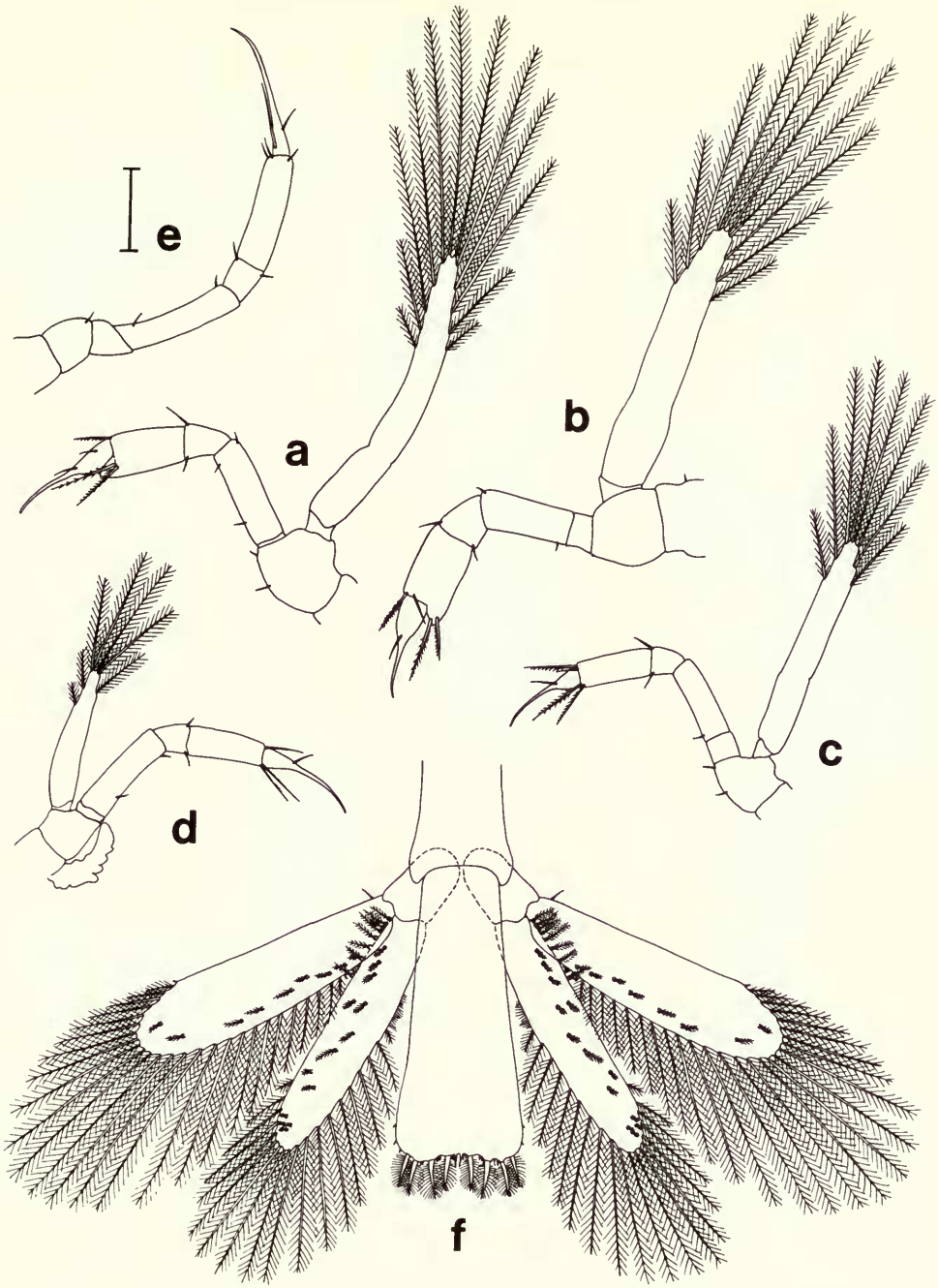

Fig. 12 Zoea 6: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) telson. Bar scale: 0·2 mm.

ZOEA 8 (Figs 16–19) 6·6 mm (5·8–7·1 mm)

Maxilliped 1 (Fig. 18a): *up to 6 plumose setae on proximo-lateral margin of exopodite.*
Pereiopod 1, 2 (Figs 18d, e): *endopodite with internal distal margin produced forward to over half length of dactylus* (excluding terminal setae).
Telson (Fig. 19i): *posterior margin convex.*

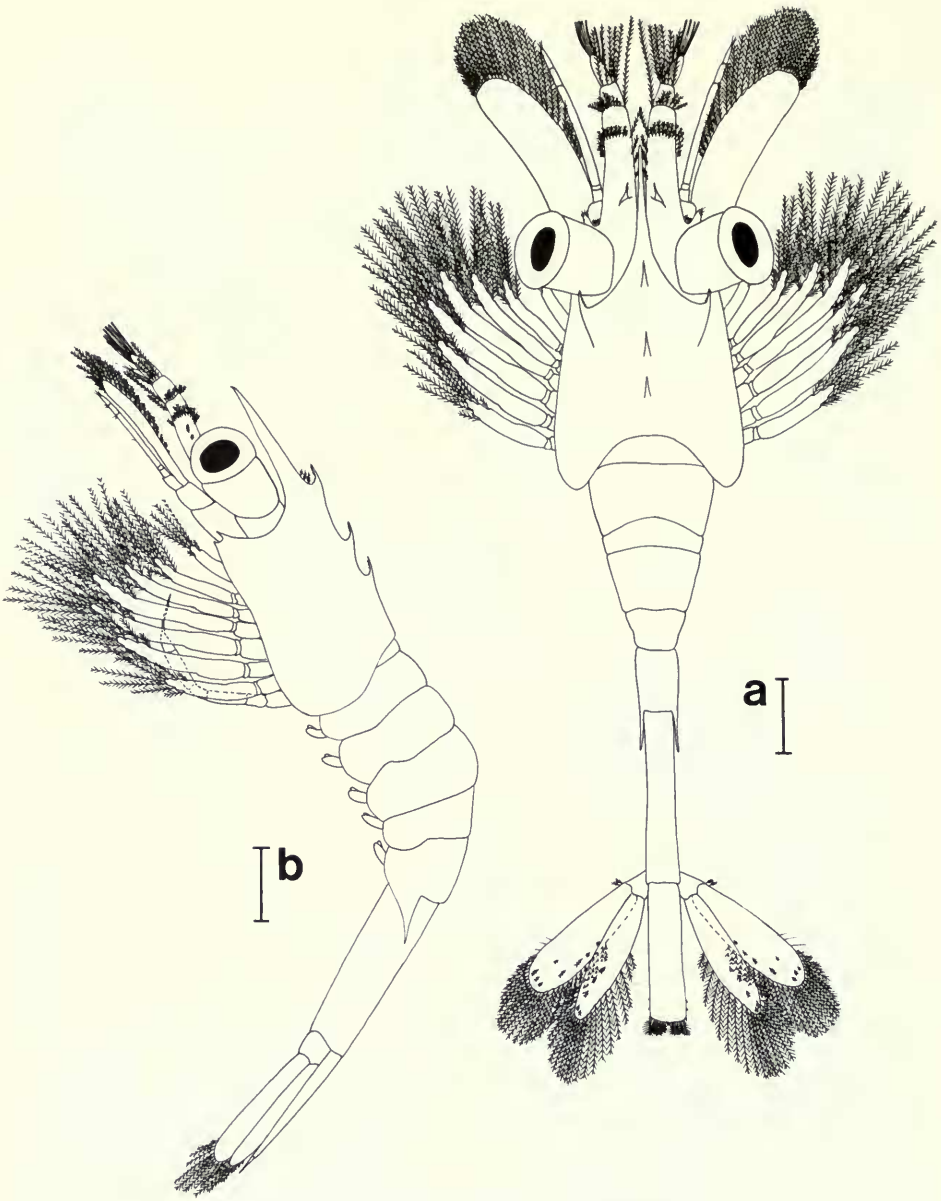

Fig. 13 Zoea 7: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

Zoea 9 (Figs 20–23) 7·3 mm (6·9–7·9 mm)

Carapace (Fig. 20b): *3 short plumose setae in angle of anterior dorso-medial spine, 1 in angle of second dorso-medial spine.*

Antenna 1 (Fig. 21a): internal flagellum of 1 or 2 segments, *external flagellum of 2 segments;* 3 or 4 groups of aesthetascs on internal margin of external flagellum; *statocyst fully developed.*

Antenna 2 (Fig. 21b): increase in number of segments of endopodite flagellum, *now longer than scathocerite.*

Maxilliped 1 (Fig. 21g): *14 to 20 setae on internal margin of basis, 5 to 9 plumose setae on proximo-lateral margin of exopodite.*

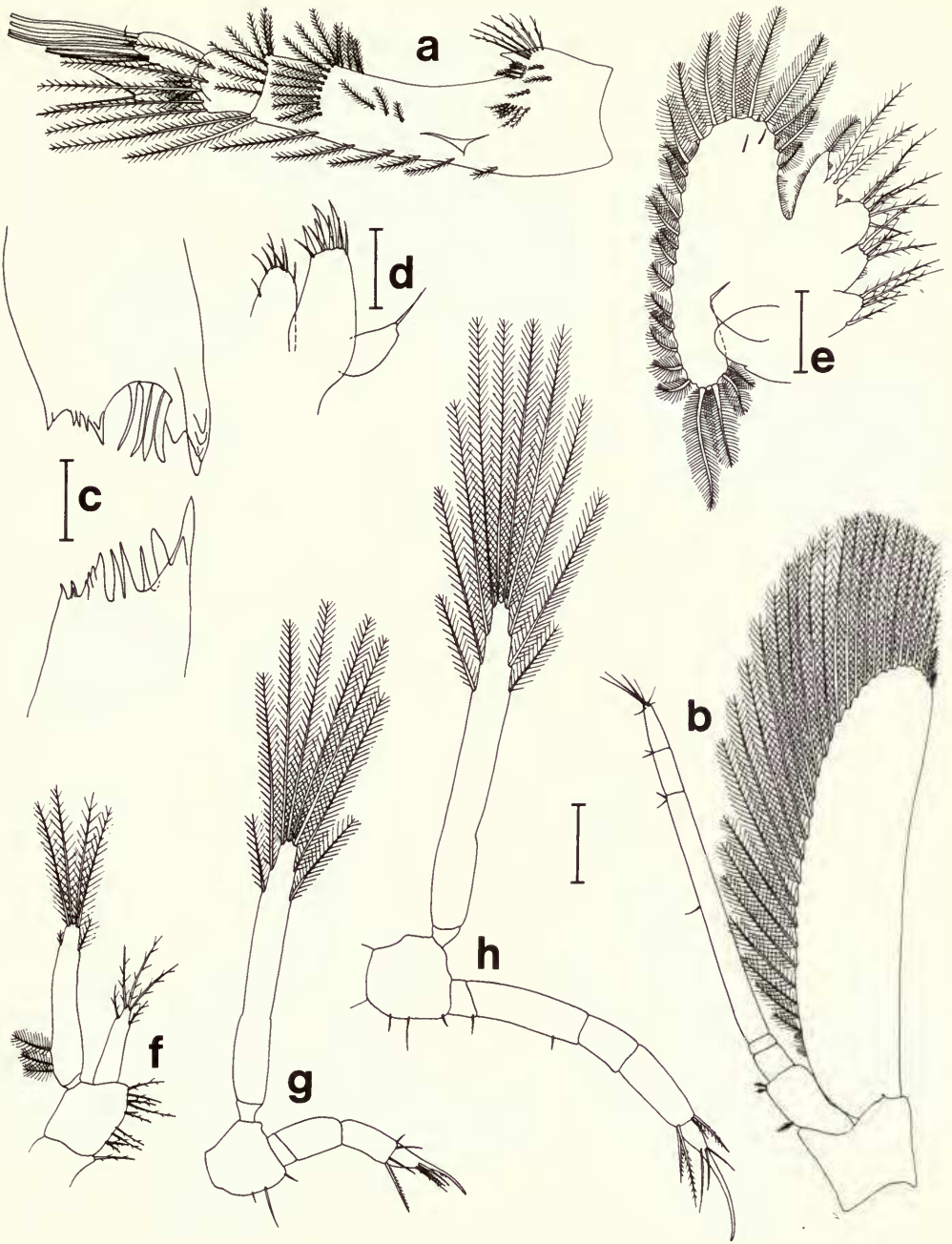

Fig. 14 Zoea 7: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a, b, f–h = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

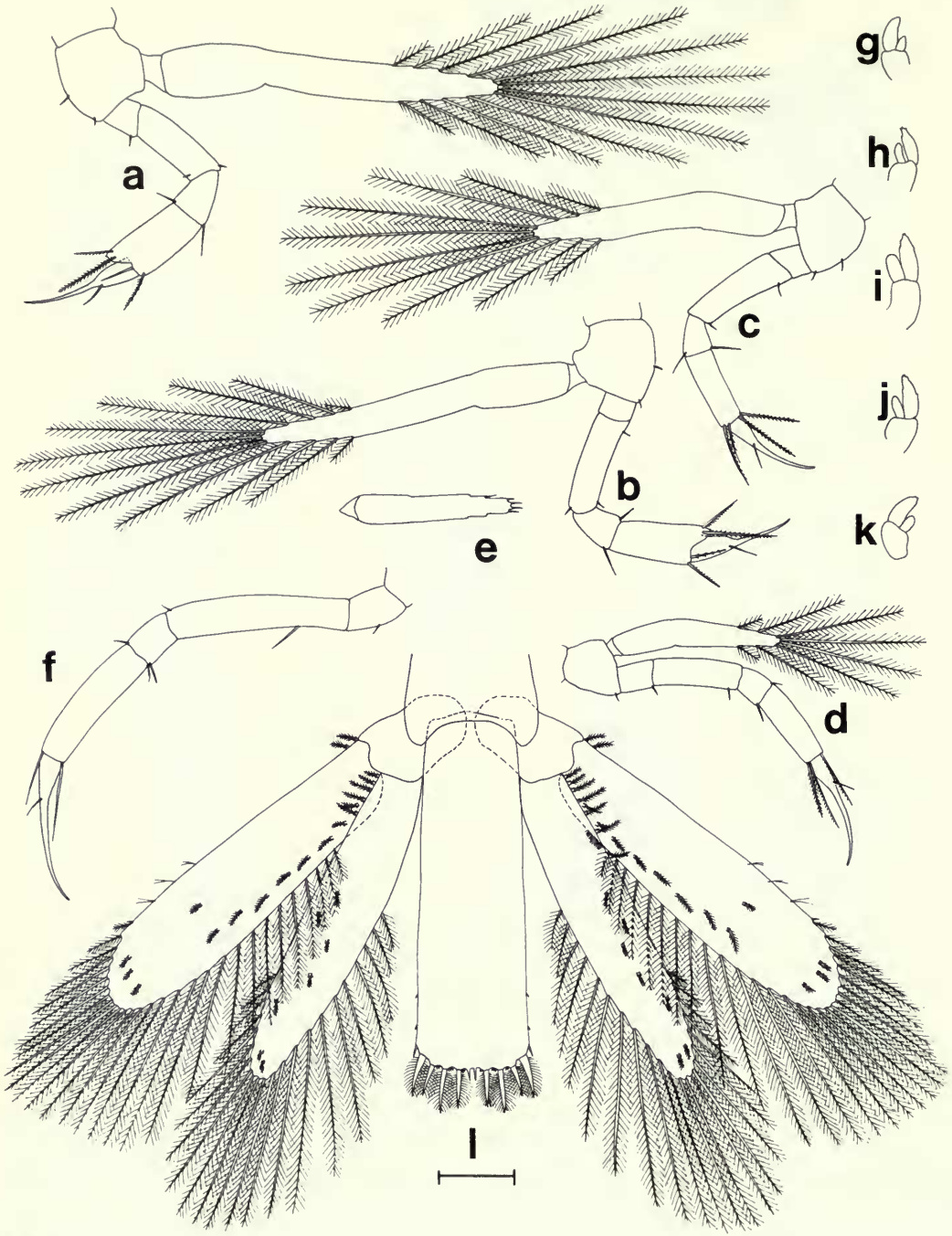

Fig. 15 Zoea 7: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) variant of pereiopod 4 exopod with reduced setae; (f) pereiopod 5; (g) pleopod 1; (h) pleopod 2; (i) pleopod 3; (j) pleopod 4; (k) pleopod 5; (l) telson. Bar scale = 0·2 mm.

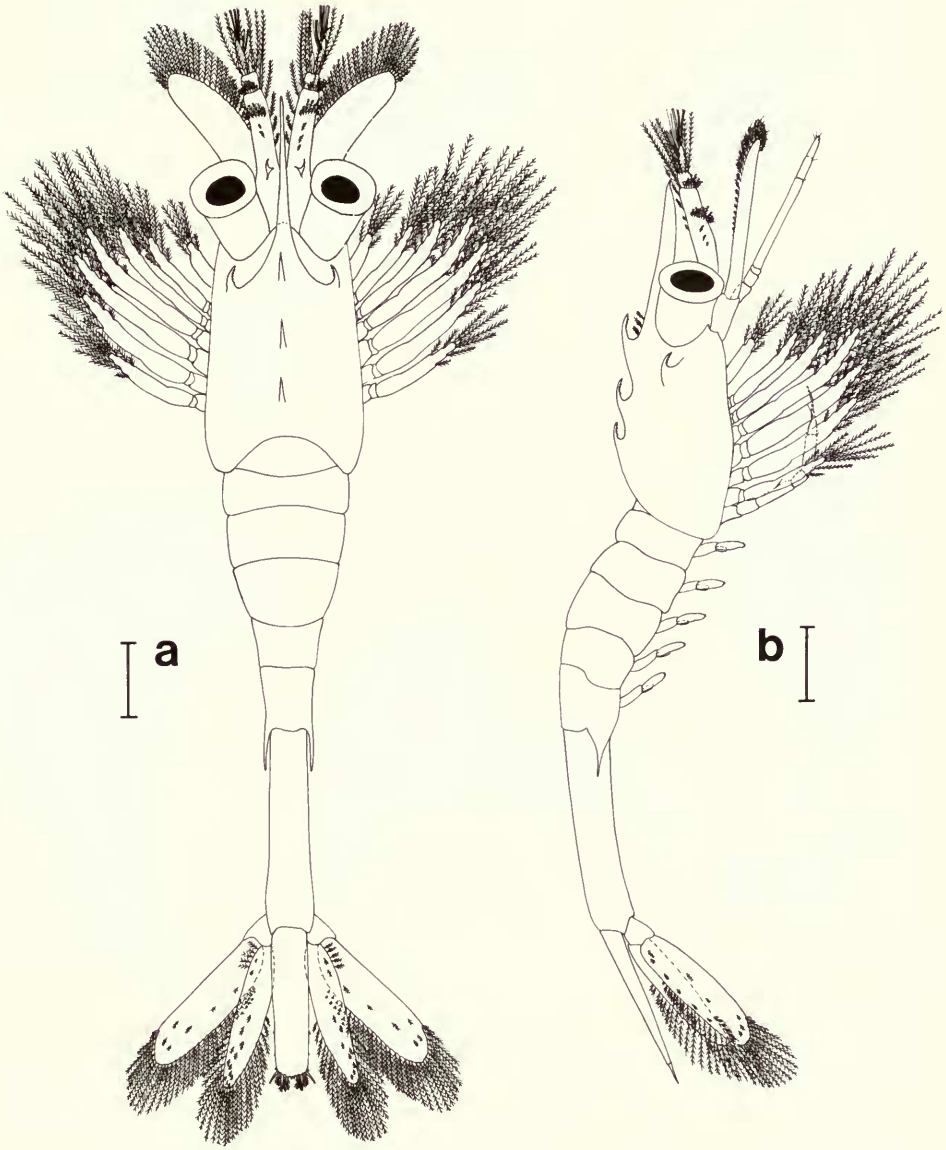

Fig. 16 Zoea 8: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

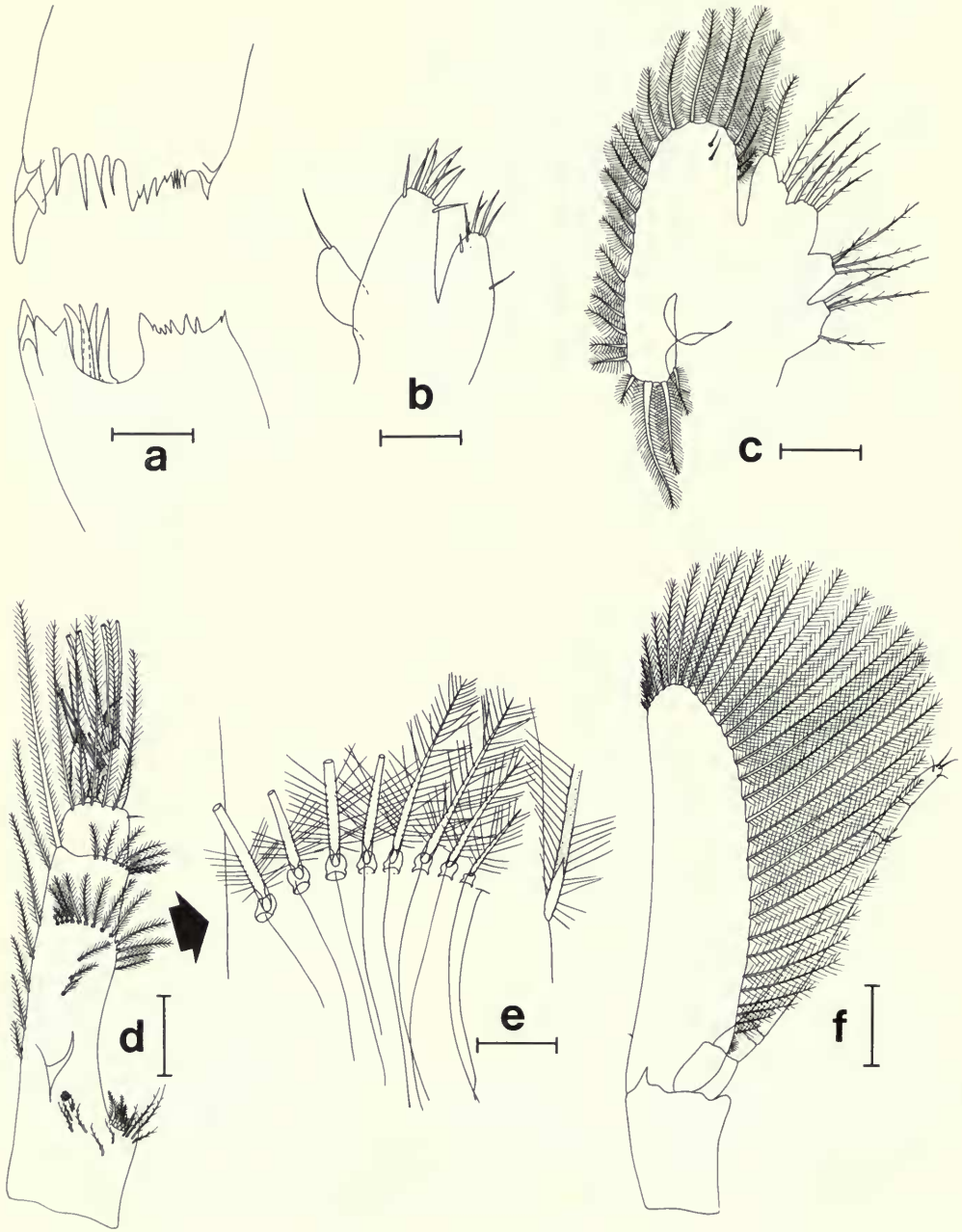

Fig. 17 Zoea 8: (a) mandibles; (b) maxilla 1; (c) maxilla 2; (d) antenna 1; (e) antenna 1 – enlargement of proximal array of sensory hairs showing thread-like connections remaining in cast exoskeleton; (f) antenna 2. Bar scales: a, e = 0·05 mm; b, c = 0·1 mm; d, f = 0·2 mm.

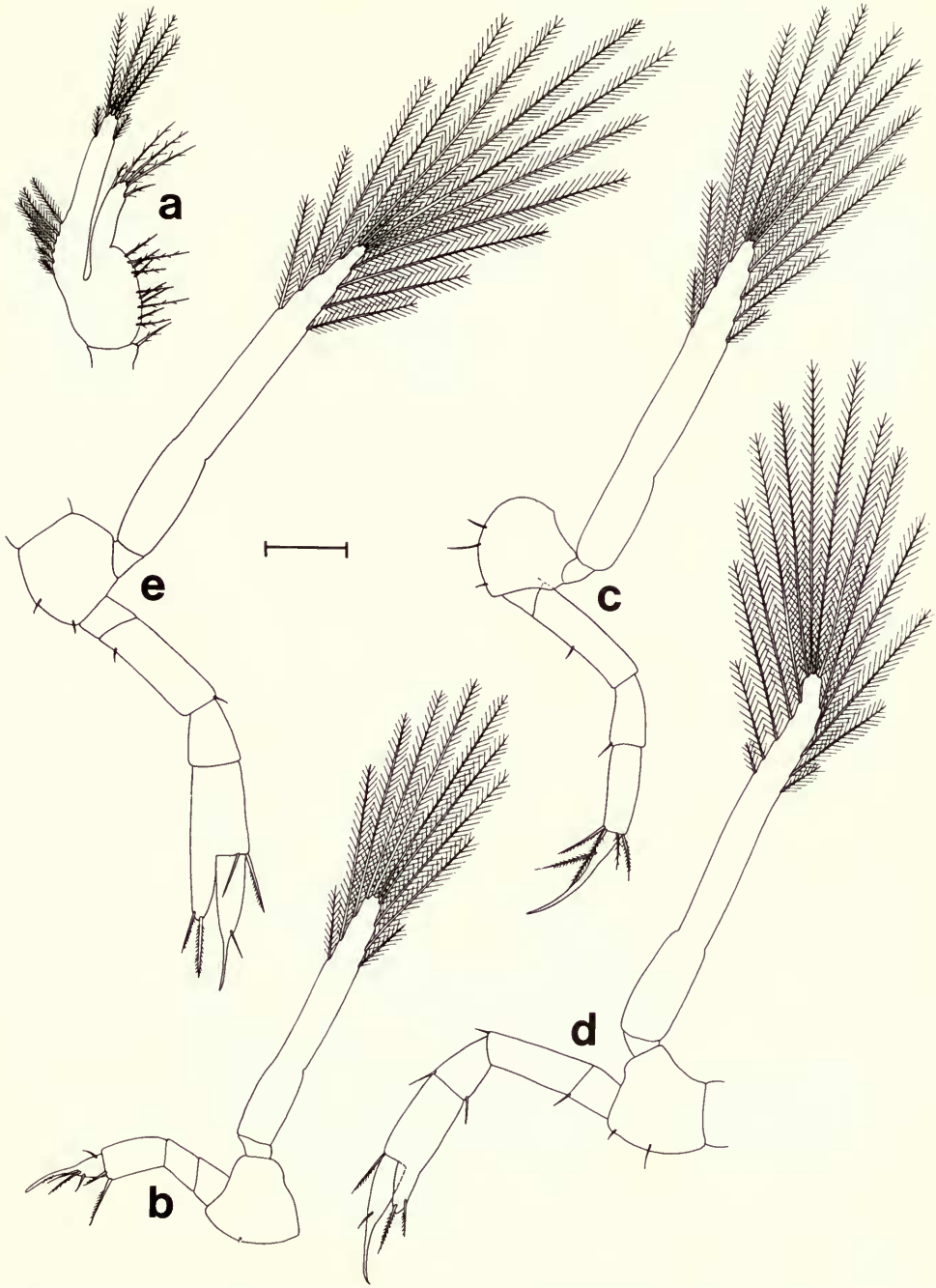

Fig. 18 Zoea 8: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2. Bar scale: 0·2 mm.

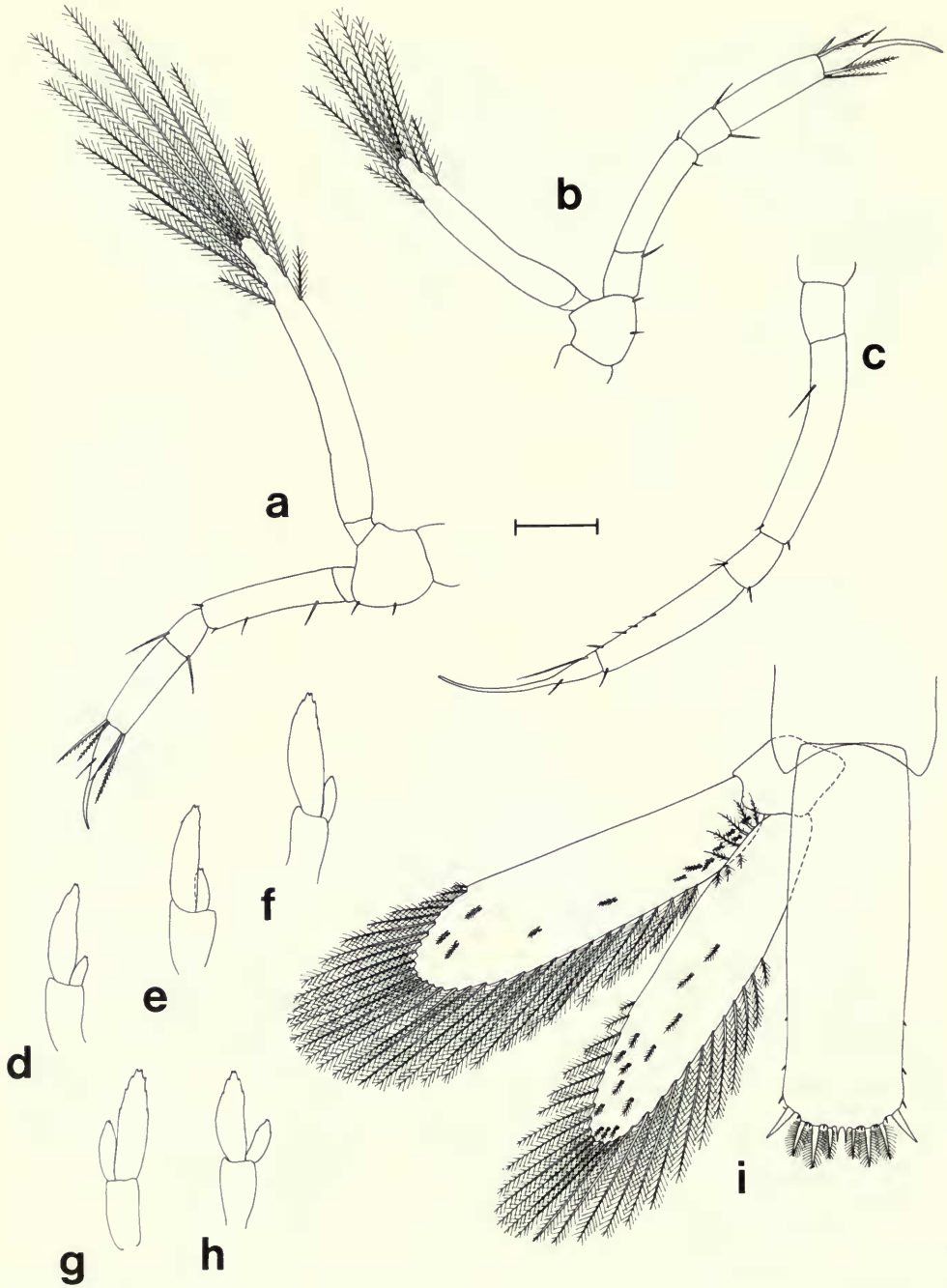

Fig. 19 Zoea 8: (a) pereiopod 3; (b) pereiopod 4; (c) pereiopod 5; (d) pleopod 1; (e) pleopod 2; (f) pleopod 3; (g) pleopod 4; (h) pleopod 5; (i) telson. Bar scale: 0·2 mm.

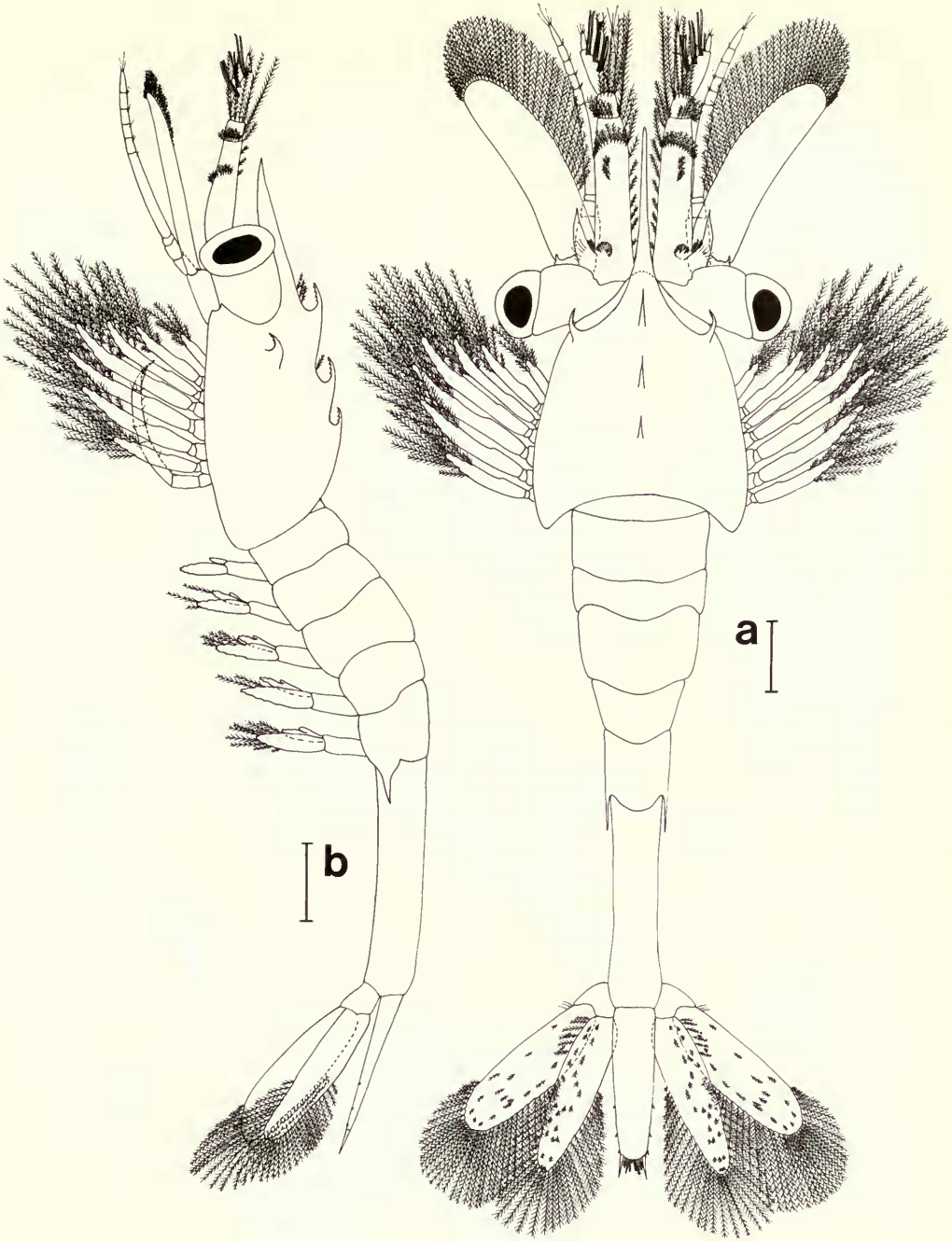

Fig. 20 Zoea 9: (a) dorsal view; (b) lateral view. Bar scales: 0·5 mm.

Pereiopods 1, 2 (Figs 22c, d): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae)
Abdomen (Figs 20b, 23c–g): *pleopods with rudimentary setae, a few fully plumose; endopodite of pleopods 2 to 5 with rudiment of appendix interna* (stylamblys).
Telson (Fig. 23h): *further narrowing distally, posterior margin with 4+4 large spines (no small spines between)* and with 3 reduced spines on latero-distal margin.

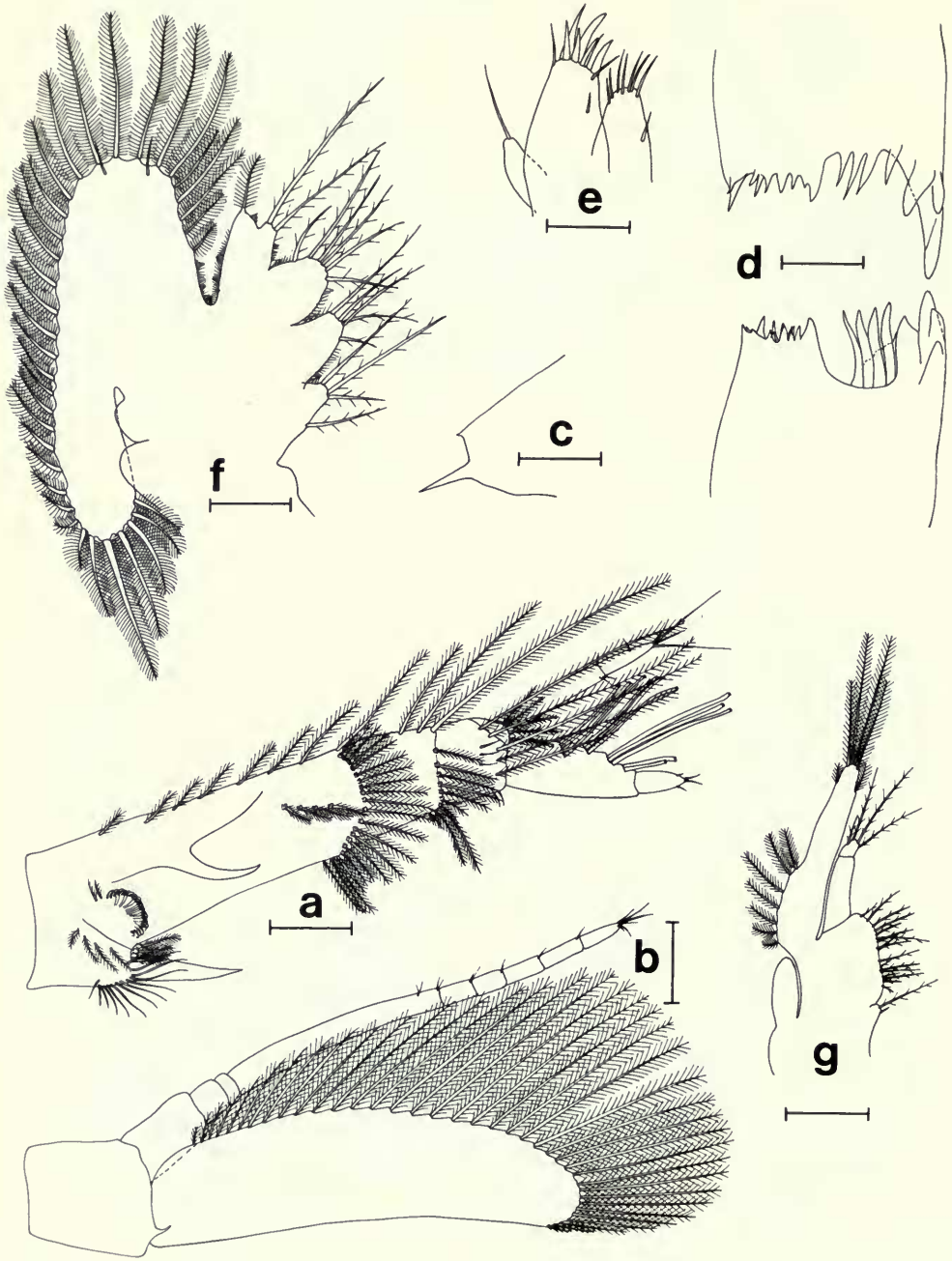

Fig. 21 Zoea 9: (a) antenna 1; (b) antenna 2; (c) antero-lateral teeth of carapace; (d) mandibles; (e) maxilla 1; (f) maxilla 2; (g) maxilliped 1. Bar scales: a, b, g=0·2 mm; c, d=0·05 mm; e, f=0·1 mm.

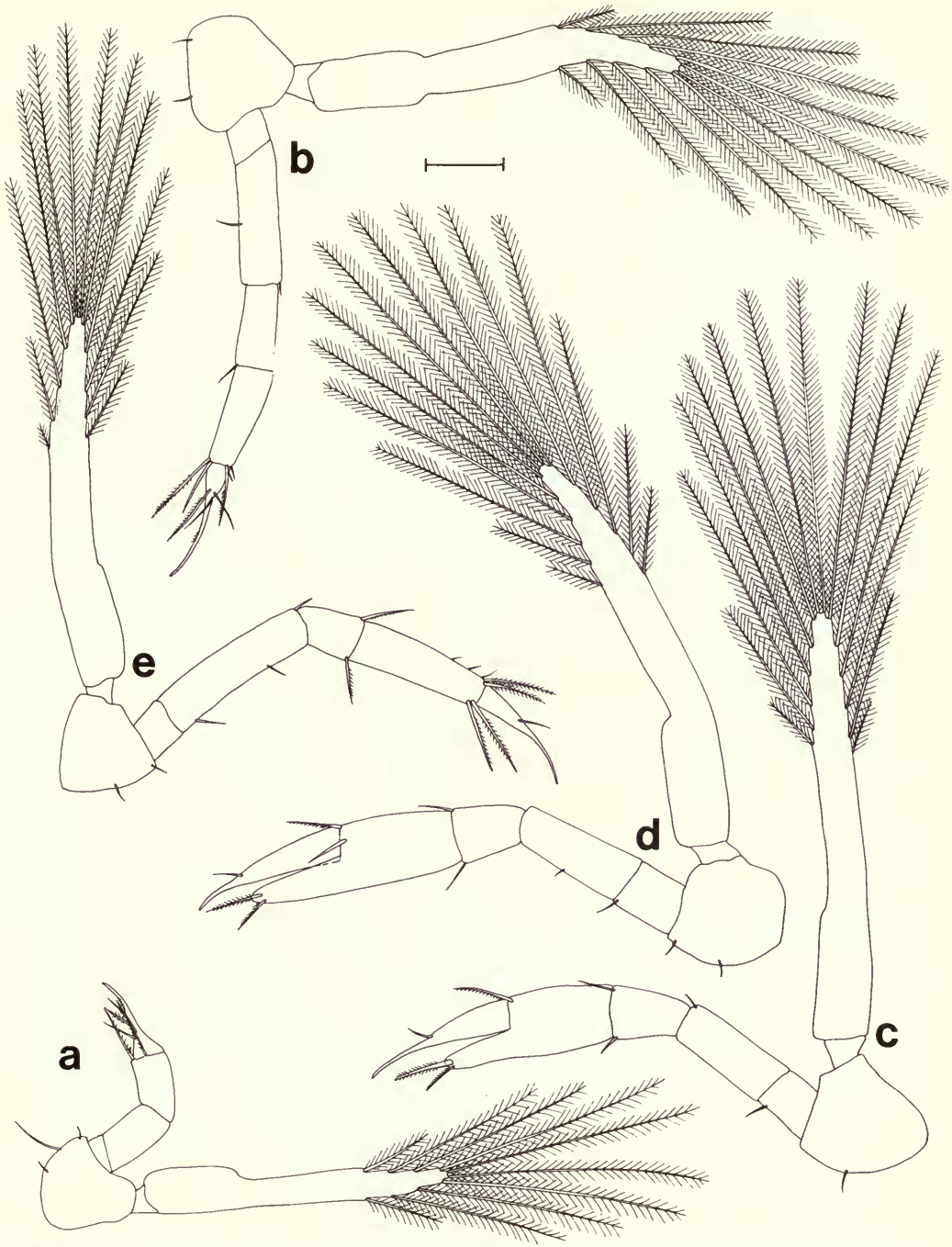

Fig. 22 Zoea 9: (a) maxilliped 2; (b) maxilliped 3; (c) pereiopod 1; (d) pereiopod 2; (e) pereiopod 3. Bar scale = 0·2 mm.

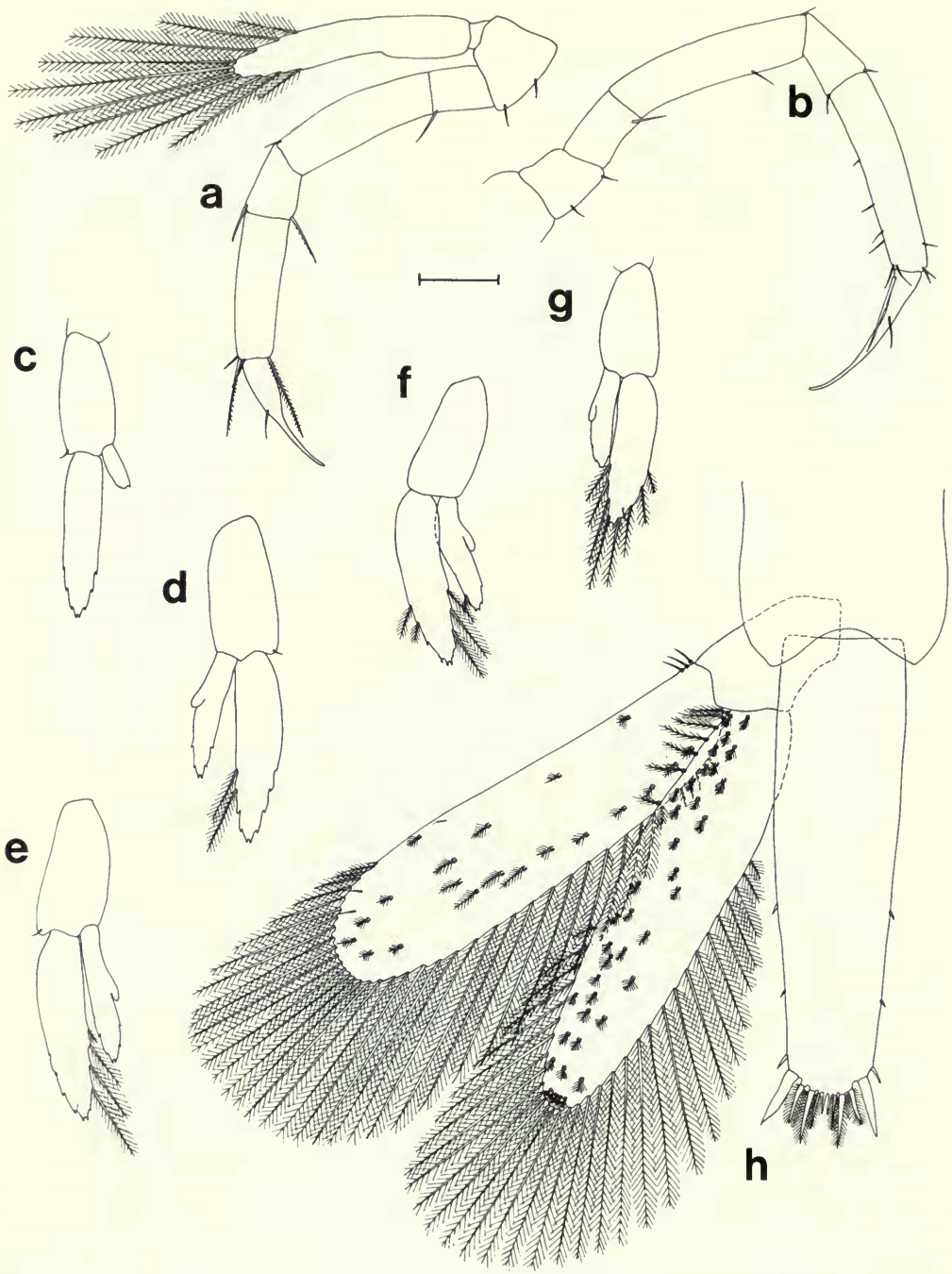

Fig. 23 Zoea 9: (a) pereiopod 4; (b) pereiopod 5; (c) pleopod 1; (d) pleopod 2; (e) pleopod 3; (f) pleopod 4; (g) pleopod 5; (h) telson. Bar scale: 0·2 mm.

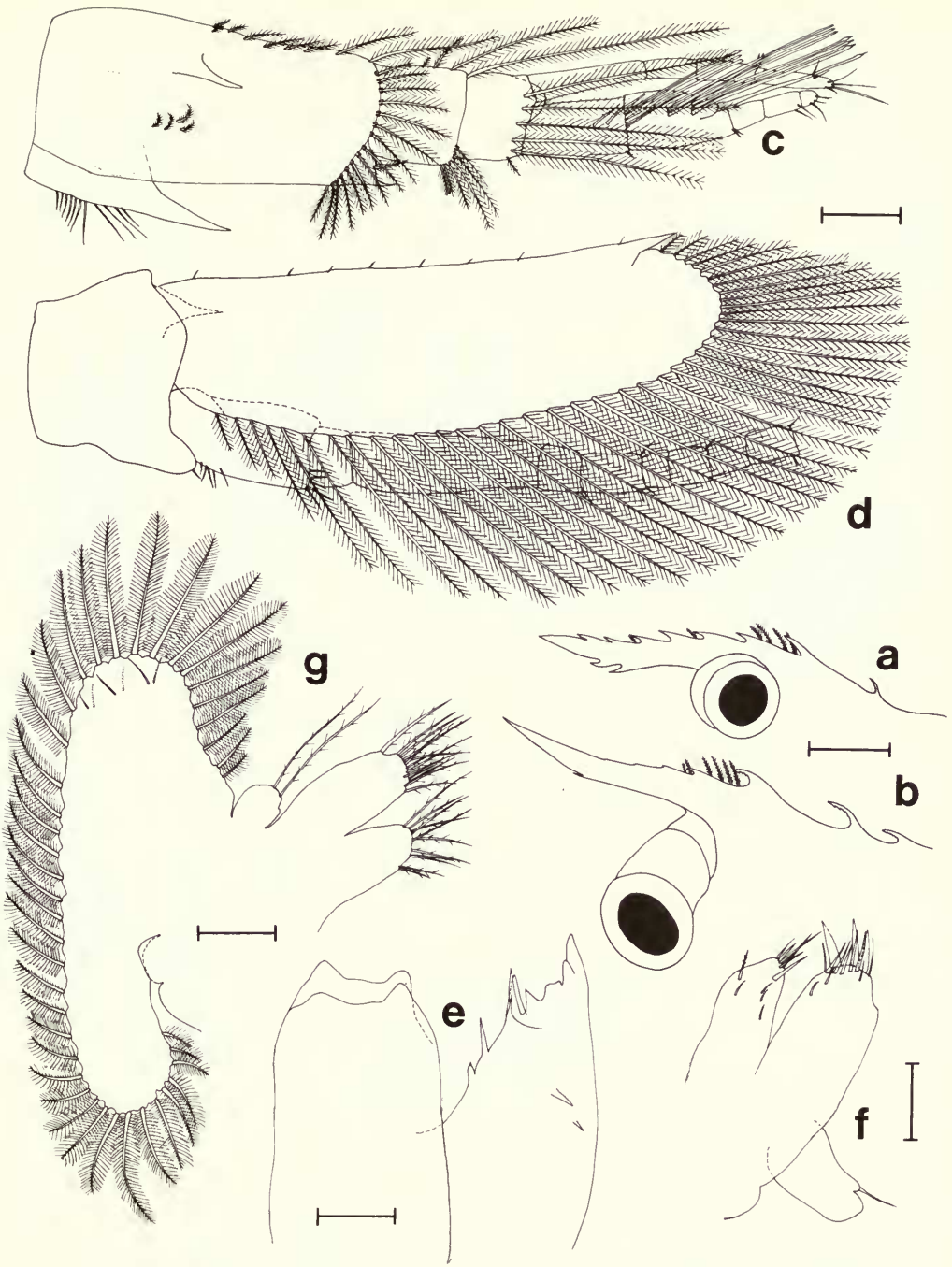

Fig. 24 Post larva 1: (a) rostrum; (b) rostrum with characters intermediate between larval and post larval phases; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

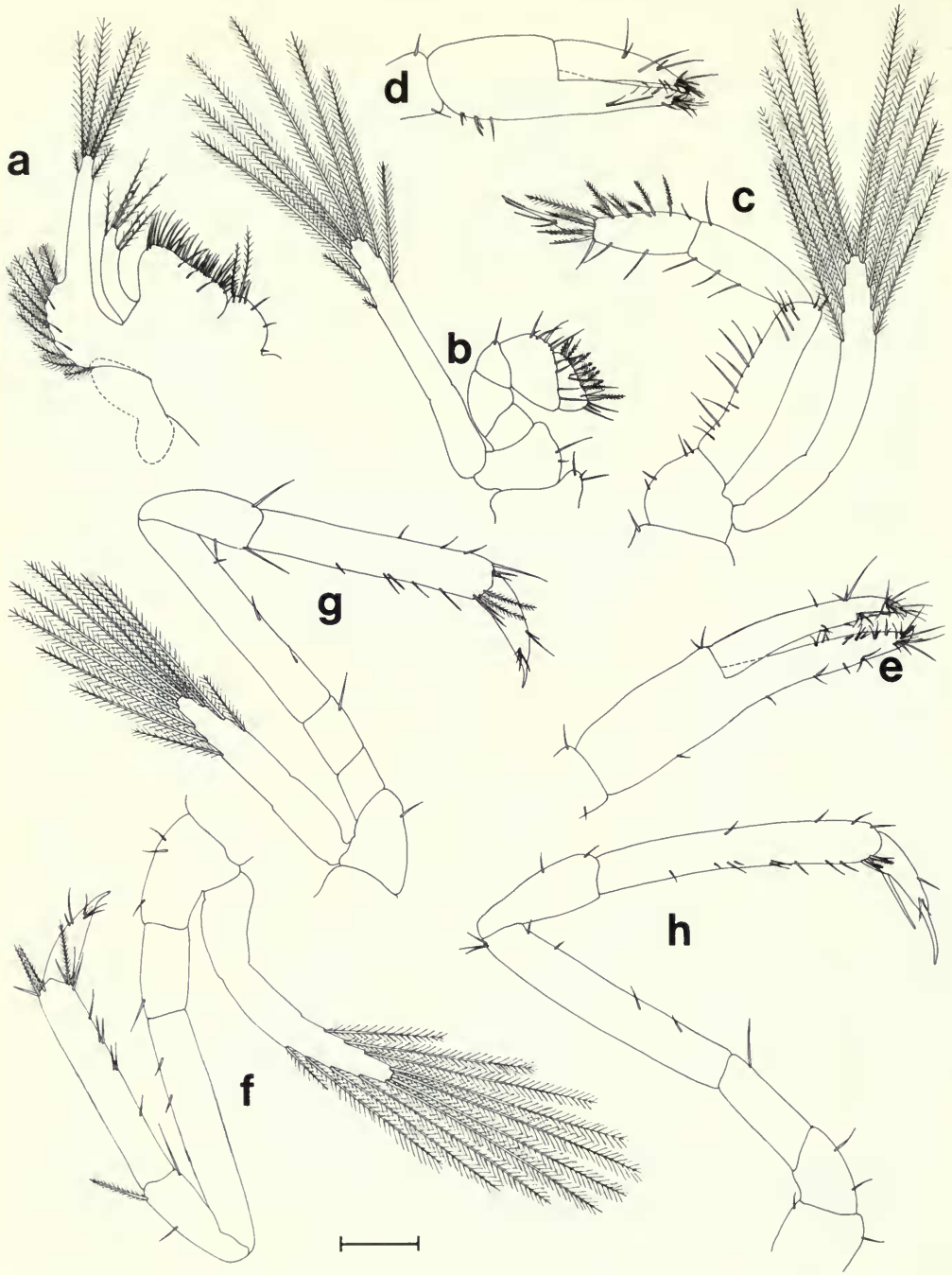

Fig. 25 Post larva 1: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1 chela; (e) pereiopod 2 chela; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5. Bar scale: 0·2 mm.

POST LARVA 1 (Figs 24–26) 7·9 mm (7·0–8·6 mm)
Most specimens had metamorphosed to post larvae or intermediate stages at this moult. Meristic characters of the more advanced individuals are described here and included in Table 1.

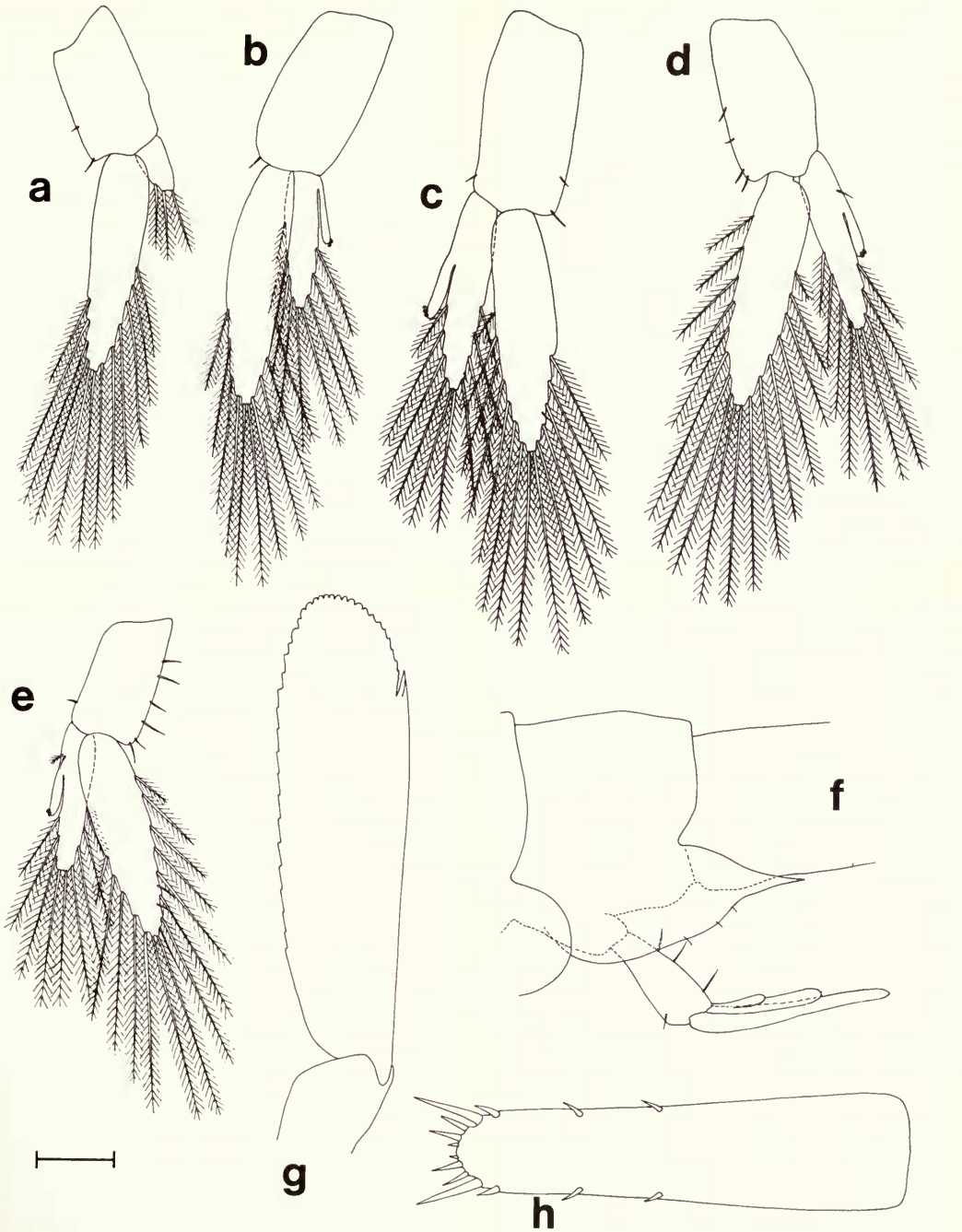

Fig. 26 Post larva: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) somite 5 with postero-lateral spines (plumose setae of pleopod 5 not shown); (g) uropod exopodite (plumose setae not shown); (h) telson. Bar scale: 0·2 mm.

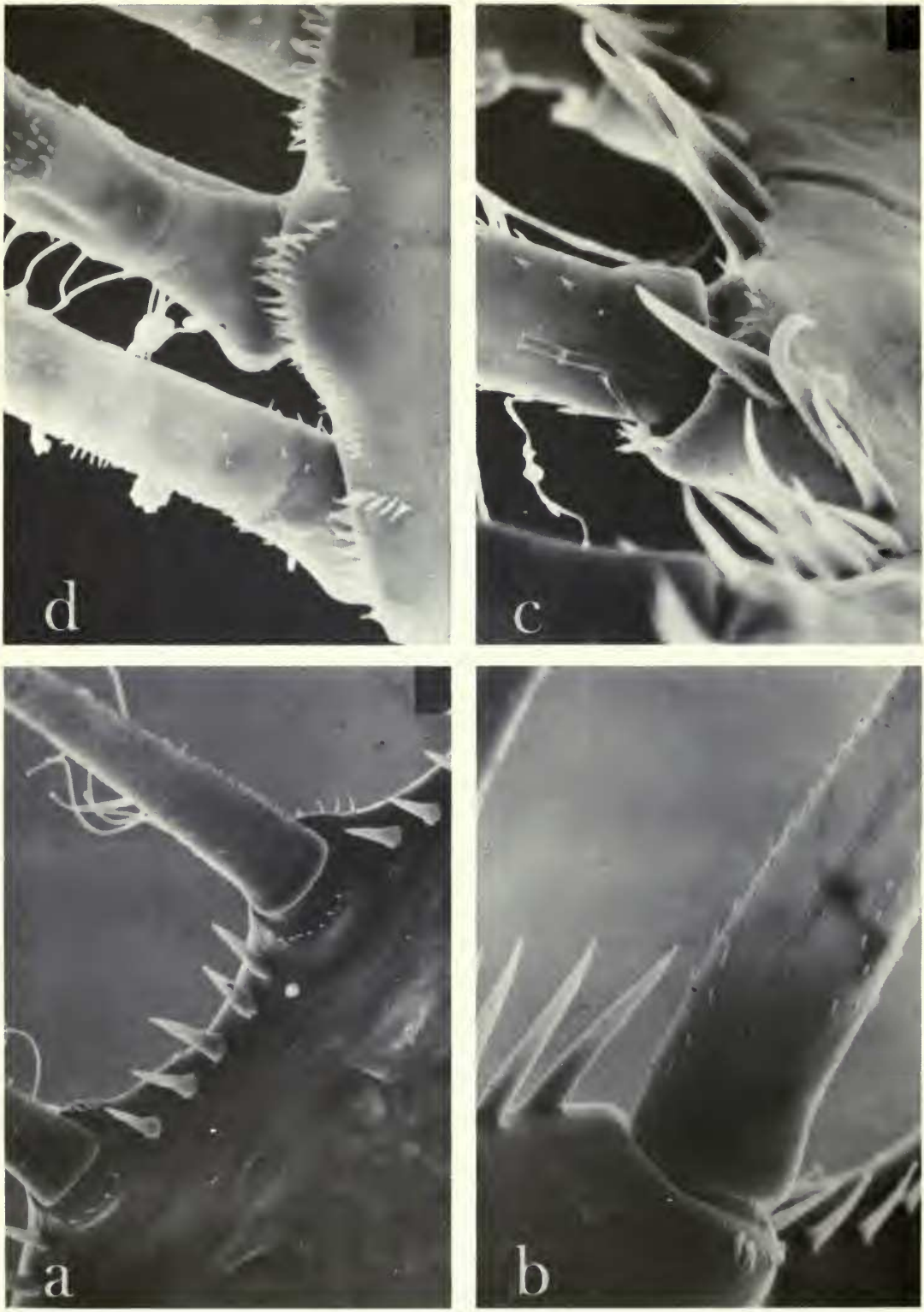

Fig. 27 Telson of palaemonid Zoea 1. (a) Dorsal view of posterior margin. Bases of large plumose spines with row of smaller spines between. (b) Single large spine ornamented with spinules. (c) Articulation at base of large spines with circlet of small spines. (d) Ventral view of posterior margin showing rows of small spines arranged with gaps.

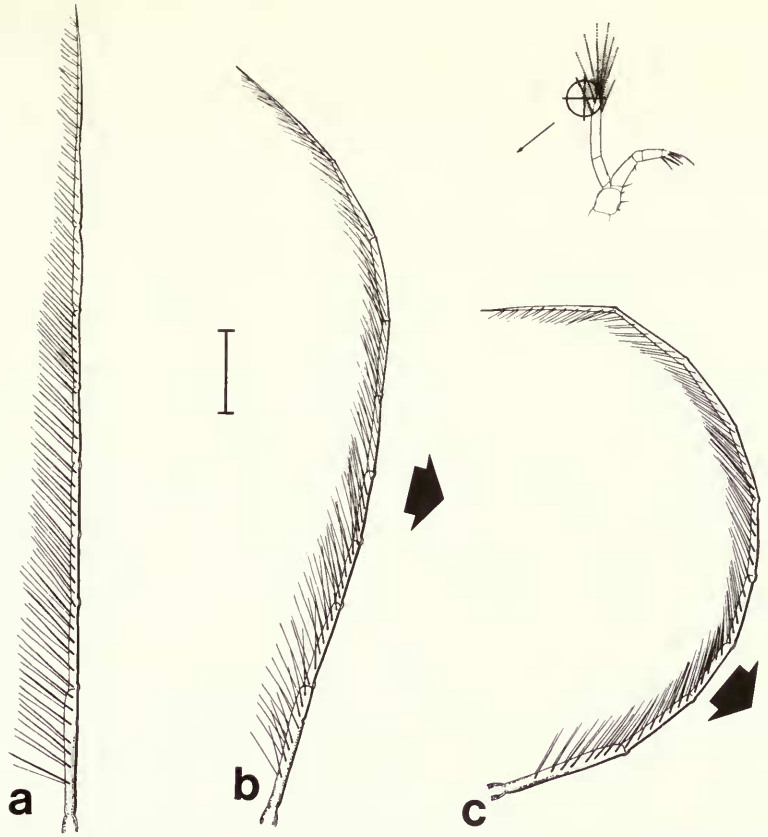

Fig. 28 Single plumose seta from natatory exopodite of pereiopod. Shaft is a differentially thickened cylinder hinged at intervals and bears two rows of thin lateral setules. (a) Seta stationary. (b) Beginning of recovery stroke. (c) End of recovery stroke. Bar scale: 0·05 mm.

Carapace (Fig 24a): *rostrum with 6 or 7 dorsal and 2 ventral teeth,* rostral tip straight. *Supra-orbital spines missing.* Intermediate condition of rostrum shown in Fig. 24b.
Antenna 1 (Fig. 24c): *internal flagellum of 5 or more segments and external flagellum of 6 or more segments.*
Antenna 2 (Fig. 24d): endopodite multisegmented, at least twice as long as scaphocerite.
Mandible (Fig. 24e); *divided into pars incisiva and pars molaris,* lacinia mobilis no longer present and palp (three jointed in adult) not yet appeared.
Maxilla 2 (Fig. 24f): reduction of setae on coxal endite and endopodite, increase in setae on basal endites.
Maxilliped 2 (Fig. 25b): endopodite with dactylus, propodus and merus flattened.
Maxilliped 3 (Fig. 25c): endopodite dactylus shortened.
Pereiopods 1, 2 (Figs 25d, e): *immovable finger of propodus same length as dactylus.*
Pereiopods 3, 4 (Figs 25f, g): dactylus shortened.
Pleopod 1 (Fig. 26a): *ratio of endopodite to exopodite 1:4;* endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.
Pleopods 2–5 (Figs 26b–e): endopodite over half length of exopodite, both with long, marginal plumose setae, endopodite with appendix interna bearing well developed interodistal coupling hooks.
Abdomen (Fig. 26f): fifth abdominal somite with posterior margin still produced into pair of lateral spines.

Telson (Fig. 26g): intermediate condition (extreme narrowing with posterior margin tapering to point not yet developed).

Discussion

Most of the specimens reared by Sollaud (1912) at the Marine Laboratory in Roscoff reached metamorphosis after 8 larval stages. But he found also '. . . quelques individus, en effet, peuvent présenter un stade IX supplementaire avant de se transformer. . .' He concluded, however, that the normal larval development for *Palaemon serratus* was eight stages (Sollaud, 1923). In the present work the differences between stages 8 and 9 were slight and confirm, therefore, the conclusion reached by Sollaud. The insertion of extra moults which probably represents an adaptation to sub-optimal conditions by prolonging larval existence is a recurrent feature of the development of Palaemoninae (Fincham, 1977, 1979). Sandifer and Smith (1979) indicated that in addition to being affected by environmental factors the tendency of individual palaemonid larvae to pass through a given number of larval stages may be inherited. They suggested also that variation in development may enhance the general advantages of an extended planktonic larval phase, a common feature of 'r' strategists. These include greater potential for dispersion and the ability to colonize new habitats quickly if favourable conditions occur. A variable planktonic existence may produce a wider spread of individuals of a given brood and average the risks of survival. At the population level Sandifer and Smith emphasize that early metamorphosis will enhance the possibility of gene flow between populations.

Many environmental factors affect development including photoperiodicity. Wickins (1972) reported work on larval *Palaemon serratus* in which growth was improved and metamorphosis reached sooner in those reared in continuous light. Eight hours dark and 16 hours light produced improved growth compared with 8 hours light and 16 hours dark; continuous darkness produced slowest growth and development. Dalley (1979) working with *Palaemon elegans* concluded that greatly increased mortality during larval development in non-circadian light regimes was due to desynchronization of the circadian rhythms of metabolic processes.

One feature commonly found in exuviae of the various larval stages are thin strands extending from the bases of sensory hairs (see Figs 17d, e). In a paper on the ultrastructure of the antennal sensilla of the shrimp *Acetes* Ball & Cowan (1977) describe dense strands of unknown composition crossing the base of their type 1 seta, which they consider uninnervated. Tracts leading from the bases of their other four types of seta contain axons. The exact nature of the strands in the exuviae of *Palaemon serratus* is not clear and will be examined further.

Swimming: adaptations and a mechanism

When palaemonid larvae first hatch they usually swim upside down and telson first. At rest the larvae tend to sink and there are several adaptations which slow the rate of descent. At either end of the body plumose setae or spines increase drag. Fringing plumose setae effectively double the area of the broad exopodite (scaphocerite) of antenna 2 at the anterior end of the body (Figs 1a, 2a, 3a, 5a, 7a, 10a, 13a, 16a, 20a). These antennal setae are thickened at the base (Fig. 4c) and their rigidity increases drag when the exopodites are spread.

At the posterior end the telson bears stout spines which are ornamented with rows of small spines and are also plumose (Figs 27a–d). The function of the ornamentation is uncertain but might further slow the rate of sinking. Body size increases as larval development progresses and the importance of even the large spines on the telson for increasing drag, diminishes when the sixth abdominal segment develops its appendages. The exopodites of these uropods

appear at zoea 3 (Fig. 41) and endopodites at zoea 4 (Fig. 6k) and are broad and flat and fringed with plumose setae. The spreading of these uropods slows the rate of sinking during periods when the larva is not swimming.

The telson, however, retains its important function as a stabilizing hydrofoil throughout larval life and is supplied with powerful muscles that enable it to assist in orientation control. Its gradual transformation from a triangular shape at zoea 1 with a 7+7 spine formula (Figs 1m, 27a–d) to the narrow shape at the last larval stage with spine formula 4+4 and three pairs of lateral spines (Fig. 23h) accompanies the gradual development of more thoracic natatory exopodites.

In the present rearing programme food is supplied to the larvae in the form of *Artemia* nauplii. In the wild it is likely that copepods and other small planktonic organisms form the main source of food (Sollaud used copepods in his rearing work at Roscoff). The pursuit of prey – *Artemia* or copepods – necessitates accurate orientation and direction control. The propulsive locomotory force is provided by the natatory exopodites developed sequentially. Zoea 1 has only three natatory exopodites – those of the maxillipeds – but biramous pereiopods are developed later and are also integrated into a regular beating pattern of the limbs. Pereiopod 5 is in fact developed by stage 4 before pereiopod 4 in *Palaemon serratus* but has no exopodite and is therefore not involved in larval swimming. The effective area of the propulsive exopodites is extended by the fringing plumose setae. Preliminary analysis of the swimming action from cine film shows that there is a power stroke and a recovery stroke. The morphological adaptations of these plumose setae and their role in swimming behaviour was determined following the routine examination by light microscopy of hundreds of moults during the course of the rearing programme.

The shaft of the plumose setae fringing the natatory exopodites is a differentially thickened cylinder with flexible cuticular hinges at intervals along its length (Fig. 28a). The hinges only permit bending towards the unthickened side of the shaft. During the propulsive power stroke the setae remain straight with the two rows of thin, lateral setules set at an obtuse angle to the shaft, thus providing maximum surface area and purchase in the water. On the recovery stroke the flexible exopodite bends and the marginal plumose setae fold back along the many hinge lines with their thin side branches streaming out behind. This offers the least possible resistance by the exopodite to the water and repositions the limb ready to begin the next power stroke.

The rhythmic beating of the six pairs of setose thoracic exopodites in the three larval stages, and swimmerets or pleopods in the post larvae of lobsters, has been analysed from cine film by Neil *et al.* (1976), Macmillan *et al.* (1976) and Laverack *et al.* (1976). No comparable study has been made for a caridean with regular sequential addition of limbs (in lobsters all limbs are present on hatching). The rarity of palaemonid larvae in the plankton remains an enigma especially as they are apparently so well adapted for swimming. Detailed analyses of cine film of swimming in larval palaemonids, together with plankton sampling using a static bottom net and experimental work on the periodicity of larval swimming, all of which are in progress, should shed some light on the problem.

References

Adensamer, T. 1898. Decapoden gesammelt auf S.M. Schiff Pola in den Jahren 1890–1894. Berichte der Commission für Erforschung des östlichen Mittelmeeres. XXII Zoologische Ergebnisse. XI. *Denkschr. Akad. Wiss. Wien* **65** : 597–628.

Ball, E. E. & Cowan, A. N. 1977. Ultrastructure of the antennal sensilla of *Acetes* (Crustacea, Decapoda, Natantia, Sergestidae). *Phil. Trans. R. Soc. Lond.* B **277** : 429–456.

Couch, R. Q. 1845. On the metamorphosis of the crustaceans, including the Decapoda, Entomostraca and Pycnogonidae. *Rep. R. Cornwall polytech. Soc.* **12** : 17–46.

Czerniavsky, W. 1884. Crustacea Decapoda Pontica littoralia, Materialia ad Zoographiam Ponticam comparatum. II. *Trans. Soc. Univ. Kharkow*, **13** (suppl.) : 1–268.

Dalley, R. 1979. Effects of non-circadian light cycles on the survival and development of *Palaemon elegans* Rathke reared in the laboratory. In: *Proc. 13th Eur. mar. Biol. Sym.* **13** : 157–163 (Eds E. Naylor & R. Hartnoll. Oxford: Pergamon Press).

Edwards, H. Milne 1837. *Histoire naturelle des Crustacés.* II. Paris. 531 pp.

Fincham, A. A. 1977. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 1. Laboratory methods and a review of *Palaemon (Palaeander) elegans* Rathke, 1837. *Bull. Br. Mus. nat. Hist.* (Zool.) **31** (1) : 1–28.

—— 1978. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 2. *Palaemonetes (Palaemonetes) varians* (Leach, 1814) and morphological variation. *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (2) : 163–182.

—— 1979. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 3. *Palaemon (Palaemon) longirostris* H. Milne Edwards, 1837 and the effect of antibiotic on morphogenesis. *Bull. Br. Mus. nat. Hist.* (Zool.) **37** (1) : 17–46.

Fincham, A. A. & Williamson, D. I. 1978. Crustacea, Decapoda: Larvae. VI Caridea, Families Palaemonidae and Processidae. *Ficht. Ident. Zooplancton,* 159/160: 8 pp.

Forward, R. B. & Cronin, T. W. 1978. Crustacean larval phototaxis: possible functional significance. In: *Proc. 12th Eur. mar. Biol. Sym.* **12** : 253–261 (Eds D. S. McLusky & A. J. Berry. Oxford: Pergamon Press).

Foxon, G. E. H. 1934. Notes on the swimming methods and habits of certain crustacean larvae. *J. mar. biol. Ass. U.K.* **19** : 829–849.

Gurney, R. 1942. *Larvae of decapod Crustacea.* 306 pp. Ray Society, London.

Hardy, A. C. & Bainbridge, R. 1954. Experimental observations on the vertical migrations of plankton animals. *J. mar. biol. Ass. U.K.* **33** : 409–448.

Holthuis, L. B. 1950. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species. 1. Subfamily Palaemoninae. *Siboga Exped.* **39a** : 1–268.

Keeble, F. & Gamble, F. W. 1904. The colour physiology of the higher Crustacea. *Phil. Trans. R. Soc. Lond.* B **196** : 295–388.

Laverack, M. S., Macmillan, D. L. & Neil, D. M. 1976. A comparison of beating parameters in larval and post-larval locomotion systems of the lobster *Homarus gammarus* (L.). *Phil. Trans. R. Soc. Lond.* B **274** : 87–99.

Macmillan, D. L., Neil, D. M. & Laverack, M. S. 1976. A quantitative analysis of exopodite beating in the larvae of the lobster *Homarus gammarus* (L.). *Phil. Trans. R. Soc. Lond.* B **274** : 69–85.

Man, J. G. De 1915. On some European species of the genus *Leander* Desm., also a contribution to the fauna of Dutch waters. *Tijdschr. ned. dierk. Vereen.* Ser. 2, **XIV** : 115–179.

Mayer, P. 1877. Zur Entwicklungsgeschichte der Dekapoden. *Jena. Z. Med. Naturw.* **11** : 188–269.

Neil, D. M., Macmillan, D. L. & Laverack, M. S. 1976. The structure and function of thoracic exopodites in the larvae of the lobster *Homarus gammarus* (L.). *Phil. Trans. R. Soc. Lond.* B **274** : 53–68.

Pennant, T. 1777. *British Zoology.* **4** : 136 pp.

Reeve, M. R. 1969. Growth, metamorphosis and energy conversion in the larvae of the prawn, *Palaemon serratus. J. mar. biol. Ass. U.K.* **49** : 77–96.

Risso, A. 1816. *Histoire naturelle des Crustacés des environs de Nice.* Paris à la libraire Greque-Latine-Allemande. 175 pp.

—— A. 1826. *Histoire naturelle des principales productions de l'Europe méridionale.* **5** : 403 pp.

Russell, F. S. 1925. The vertical distribution of marine macroplankton. An observation on diurnal change. *J. mar. biol. Ass. U.K.* **13** : 769–809.

—— 1927. The vertical distribution of marine macroplankton. V. The distribution of animals caught in the ring-trawl in the daytime in the Plymouth area. *J. mar. biol. Ass. U.K.* **14** : 557–608.

Sandifer, P. A. & Smith, T. I. J. 1979. Possible significance of variation in the larval development of palaemonid shrimp. *J. exp. mar. Biol. Ecol.* **39** : 55–64.

Savage, R. E. 1926. The plankton of a herring ground. *Fish. Invest. Lond.* **9** : 1–35.

Sharp, B. 1893. Catalogue of the crustaceans in the museum of the Academy of Natural Sciences of Philadelphia. *Proc. Acad. nat. Sci. Philad.* 104–127.

Sollaud, E. 1912. Les metamorphoses du 'Bouquet', *Leander serratus* Pennant. *C. R. Acad. sci. Paris* **154** : 664–666.

—— 1921. Le comportment des larves de *Palaemonetes varians microgenitor* Boas. Changement de signe du phototropisme après la métamorphose. *Bull. Ass. fr. Avanc. Sci. Congrès de Rouen* **1921** : 671–673.

—— 1923. Le developpement larvaire des Palaemoninae. *Bull. biol. Fr. Belg.* **57** : 509–603.

Sutton, A. H., Main, G. & Ronald, A. 1969. An instrument for counting the larvae of the prawn *Palaemon serratus* and the brine shrimp *Artemia salina*. *Lab. Pract.* **18** : 433–436.

Thompson, W. V. 1836. Memoir on the metamorphosis in the Macrourae or long-tailed Crustacea, exemplified in the prawn *(Palaemon serratus)*. *Edinb. New phil. J.* **21** : 221–223.

Wickins, J. F. 1972. Developments in the laboratory culture of the common prawn *Palaemon serratus* Pennant. *Fishery Invest. Lond.* Series 2 **27** (4) : 1–23.

Williamson, H. C. 1915. Nordisches Plankton. VI. Crustacea Decapoda. Larven. *Nord. Plankt.* **6** : 315–588.

Manuscript accepted for publication 11 June 1982.